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Fishery Bulletin

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NUMERICAL INTEGRATION OF DAILY GROWTH INCREMENTS: AN EFFICIENT MEANS OF AGEING TROPICAL FISHES FOR STOCK ASSESSMENT

STEPHEN RALSTON[1] AND HAPPY A. WILLIAMS[2]

ABSTRACT

For an objective, cost-effective ageing methodology applicable to tropical species, a new approach to estimating parameters of the von Bertalanffy growth equation through the study of otolith microstructure was developed and applied to *Pristipomoides zonatus*, a deepwater snapper widely distributed throughout the Indo-Pacific region. The average width of sagittal daily growth increments was used to measure otolith growth rate, which was then related to the size of the otolith. The data were numerically integrated, providing estimates of age (in years) at regular 500 μm increments to otolith length, which was then used to predict fork length (FL mm) at age with regression analysis. The data were fitted to the von Bertalanffy growth model, resulting in $FL = 442\ (1 - \exp(-0.234\ (Age + 0.892)))$.

The method was critically examined and validated through the study of 1) annual hyaline and opaque markings that appear in the otoliths, 2) Monte Carlo simulation, 3) length-frequency analysis, 4) examination of spawning seasonality relative to back-calculated birth date taken from the time of first annulus formation, and 5) empirical comparisons with the literature concerning snapper growth.

Developing stock-assessment models tailored to the characteristics and needs of tropical fisheries is an area of active and productive research. In particular, significant progress has been made over the last several years in the area of length-based methods (Schnute and Fournier 1980; Jones 1981; Pauly 1982, 1987b; Fournier and Breen 1983; Fournier and Doonan 1987; Schnute 1987). With these advances, a powerful array of biologically realistic models is now available for analyzing length-frequency data.

Although tremendous strides have been made in developing these new length-based methods, the importance of acquiring other information besides length-frequency data and total catch statistics is all the more evident. Ancillary information usually helps to stabilize and improve the estimation of model parameters (Schnute and Fournier 1980; Fournier and Doonan 1987). Foremost is developing an independent knowledge of growth dynamics (Gulland 1987; Morgan 1987). It is now generally accepted that the analysis of length-frequency data, in conjunction with age estimates derived from the study of hard parts, represents the most promising avenue for future assessment work on exploited tropical species (Pauly 1987a).

Nonetheless, estimating growth rates of tropical species by using otoliths has been a difficult and persistent problem. Investigators have often failed in their efforts, either because of an absence of conventional hyaline and opaque markings, as is true of most tropical species, or because of an aversion to direct enumeration of daily otolith increments. The latter can be an extremely difficult, time consuming, and tedious process.

Since Pannella (1971) first discovered the existence of daily otolith increments, a large body of work has developed on the subject. While many investigators have touted the potential benefits of ageing tropical species by using otolith microstructure, few have attempted to develop growth curves with assessment goals specifically in mind. Instead, most work to date has dealt with ageing larval forms (Jones 1986) and elucidating endogenous and environmental effects on increment formation (Campana and Neilson 1985). Although much useful information has been gained, daily increments have yet to fulfill their promise with respect to applications in the area of juvenile and adult population dynamics.

The purpose of this study was to develop a general method of ageing tropical fishes by using daily

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growth increments, specifically with stock-assessment applications in mind. In this regard, the von Bertalanffy growth equation (Ricker 1979) is of fundamental importance. Due to its widespread use in assessment models (e.g., the Beverton and Holt [1957] yield formulation), parameter estimates for this equation provide an ideal complement to many of the length-based methods that are currently in use (e.g., Morgan 1987). The ultimate goal of this study was, therefore, to develop a methodology to estimate the von Bertalanffy growth parameters K and L_∞ from the study of daily increments. Ideally, the approach developed should be general in its application, easy to implement, simple in its technical requirements, and cost effective. Were such a uniform framework to the study of age and growth of exploited tropical species developed, it would assist routine assessment work greatly.

MATERIALS AND METHODS

As part of a larger program to assess stocks of deep slope fishes in the Mariana Archipelago (Polovina 1985; Polovina and Ralston 1986; Ralston in press b), a study of the age and growth of gindai, *Pristipomoides zonatus*, was initiated. This commercially important eteline snapper (Lutjanidae) is widely distributed in the Indo-Pacific region (Allen 1985) and is the most commonly caught species in Guam's deepwater hook-and-line fishery (Polovina 1986).

Field sampling for gindai specimens was conducted from the NOAA ship *Townsend Cromwell* during the 2 yr period spanning April 1982 to May 1984. During this time, six 40 d cruises were completed, such that samples of gindai were obtained during all months of the year except March, September, and October.

All gindai were caught during daylight hours by using hydraulic fishing reels equipped with circle fish hooks. When landed, fish were measured to the nearest millimeter fork length (FL) with a measuring board and weighed to the nearest 0.01 kg on a beam balance.

Specimens were sexed at the time of capture by gross examination of the gonads. In addition, a representative selection of the gonads was frozen for more detailed examination in the laboratory. There, they were preserved in a solution of 10% buffered formalin and weighed to the nearest 0.1 mg. Ovaries were staged with the classification of Everson (1984), developed for *Etelis carbunculus*, a related deepwater eteline lutjanid. His classification recognizes seven stages based on egg size, shape, and yolk content, i.e., (I) primordial, (II) early developing, (III) developing, (IV) advanced developing, (V) early ripe, (VI) ripe, and (VII) residual. Gonadosomatic indexes (gonad weight expressed as a percentage of body weight) also were calculated where possible.

Otoliths

At the time of capture, sagittal otoliths were collected, by frontal section through the cranium, from certain individuals sampled uniformly from the full size range of gindai captured. The otoliths were rinsed in fresh water to remove adhering membranes and endolymph and were stored dry in glass vials. Later in the laboratory, they were examined with a dissecting microscope for the presence of hyaline (i.e., translucent) and opaque markings while illuminated with reflected light against a dark background. When markings were present, the distance from the focus to the beginning of each opaque zone was measured along the postrostral growth axis by using a calibrated ocular micrometer. Total otolith length (focus to postrostrum) also was recorded.

A random subsample of gindai otoliths was taken, and their microstructure examined for the presence of daily increments (Campana and Neilson 1985). To prepare the otoliths, they were first embedded in casting resin, which was allowed to harden completely. Cast otoliths were sectioned on a Buehler[2] ISOMET low speed jewelry saw. Thin (0.70 mm) sections were made through the focus along a frontal plane to the most distal portion of the postrostrum. Sections were polished sequentially on a Buehler ECOMET polisher/grinder with 180 and 600 grit abrasive disks. Samples were then briefly etched for 5–30 seconds in a dilute solution of 1% HCl, washed in water, and dried. Prepared sections were mounted on glass slides with Euparol or Flotexx and cover slips and allowed to clear and harden completely prior to viewing (approximately 2 weeks).

Mounted otolith sections were examined with a compound binocular microscope by using transmitted light at a magnification of 200 or 400×. Total lengths of the otoliths (i.e., the distance in micrometers between the focus and the postrostral margin) were measured (N = 94) and individual readings were made at selected points along the postrostral growth axis, wherever it was possible to distinguish the characteristic bipartite structure of daily increments. At each site sampled the average width of presumptive daily growth increments was determined by counting a small number (me-

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

dian = 14, range = 5–22) of increments and measuring the axial length of the short segment in which they occurred. In addition, the curvilinear distance between the midpoint of each segment and the otolith focus was measured along the focus to postrostral growth axis. Up to 12 readings were made from each preparation. The focus was defined to be the most posterior of what typically were several primordia (e.g., Radtke 1987).

The data were summarized by computing the ratio of segment length in micrometers to the included number of increments at each specific site examined, providing an estimate of the average increment width at some measured distance from the otolith focus. Under the assumption that one increment forms each day, these data can be used to estimate the instantaneous growth rate of the otolith (Ralston and Miyamoto 1981, 1983; Ralston 1985).

To estimate age, a simple form of numerical integration was employed. Starting at the focus, the data were subdivided into 500 μm intervals of otolith length. For each interval, the arithmetic mean growth rate of the otolith was calculated based upon the number of readings falling therein. This average growth rate was then divided into 500 μm to estimate the number of days needed to complete growth through the intervals, which were sequentially accumulated away from the focus, and finally divided by 365.25 to convert age estimates to years. The size of the otolith upon completion of growth through each interval was used to predict the corresponding FL of the fish after the natural logarithm of FL was regressed on the logarithm of total otolith length. These data (age [in years] and FL [mm]) were then fitted to the von Bertalanffy growth equation (Ricker 1979) by using a nonlinear regression routine (SAS Institute Inc. 1979, NLIN procedure).

Monte Carlo simulation techniques (Naylor et al. 1966) were applied to this analytical procedure to evaluate the accuracy (i.e., bias) of the estimator and to study the precision of parameter estimates. The structure of the simulation model was such that von Bertalanffy growth was assumed by stipulating a decreasing linear relationship between somatic growth rate and length, i.e., $d(\mathrm{FL})/dt = K(L_\infty - \mathrm{FL})$. Likewise, the relationship between otolith length (OL) and FL was assumed to be governed by the power function, so that $\mathrm{FL} = \alpha \mathrm{OL}^\beta$. Otolith growth rate, $d(\mathrm{OL})/dt$, was then obtained by forming the ratio of $d(\mathrm{FL})/dt$ and $d(\mathrm{FL})/d(\mathrm{OL})$. All parameters in the model were otherwise set equal to the estimates obtained from the otolith study, and the specific probability distributions invoked were similar to those encountered with the actual data.

Length-Frequency Analysis

As an independent means of verifying results obtained through the study of otoliths, the regression method of Wetherall et al. (1987) was used to estimate specific growth and mortality parameters characterizing the study population. The analysis was based on the combined length-frequency distribution (FL rounded to the nearest 10 mm) of all gindai sampled (see Ralston [in press a] for a discussion of the effects of pooling length data taken at different times throughout the year).

Initially, this method requires determination of the least FL at which fish are fully represented in the catch ($\ell_{c,\min}$). For this purpose, the first size class larger than the mode was assumed to be the smallest length category fully sampled (see, for example, Ricker 1975). Moreover, for this and any larger cutoff value ($\ell_{c,i}$), we were able to compute the mean size of fully vulnerable fish in the catch ($\bar{\ell}_i$), i.e., those fish greater than $\ell_{c,i}$. As $\ell_{c,i}$ was successively advanced through the fully vulnerable size range, the mean and variance in size of larger fish were recalculated at each step, and a series of ordered pairs was developed. The actual estimation procedure involved regressing values of $\bar{\ell}_i$ against successive values of $\ell_{c,i}$. The inverse of the standard error of $\bar{\ell}_i$ was used as a statistical weight for each point, leading to the best linear unbiased estimates of the slope (δ) and intercept (ξ). With the resulting regression statistics, the formulae provided in Wetherall et al. (1987) were used to obtain point estimates of the ratio of total instantaneous mortality rate to the von Bertalanffy growth coefficient (Z/K) and the von Bertalanffy asymptotic size parameter (L_∞). In particular, they showed that $Z/K = \delta/(1 - \delta)$ and $L_\infty = \xi/(1 - \delta)$. Likewise, error estimates for these statistics were calcuated as well.

RESULTS

Age Estimation from Increment Microstructure

In all, 440 otoliths were extracted, and of these, 94 were sectioned and examined for daily increments. As expected, there is a clear statistical basis for predicting FL from OL (Fig. 1). The regression equation relating these variables is highly significant ($P < 0.0001$) and is given by

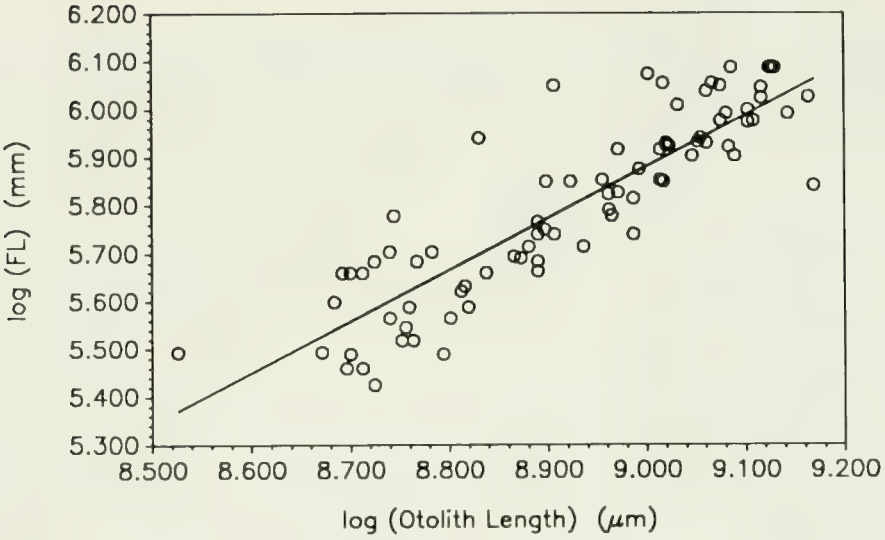

FIGURE 1.—Regression of the natural logarithm of FL on the log of otolith length (OL) (focus to distal margin of postrostrum).

$$\log(FL) = -3.783 + 1.074 \log(OL),$$

with $r^2 = 0.76$ and standard errors for the slope and intercept equal to 0.0634 and 0.5665, respectively.

The sagittae of gindai display microstructure (Fig. 2) typical of daily increments observed in other studies (Dunkelberger et al. 1980; Tanaka et al. 1981; Watabe et al. 1982). Light incremental zones and dark discontinuous zones are clearly visible in the photomicrograph. One daily growth increment is composed of the bipartite combination of a single

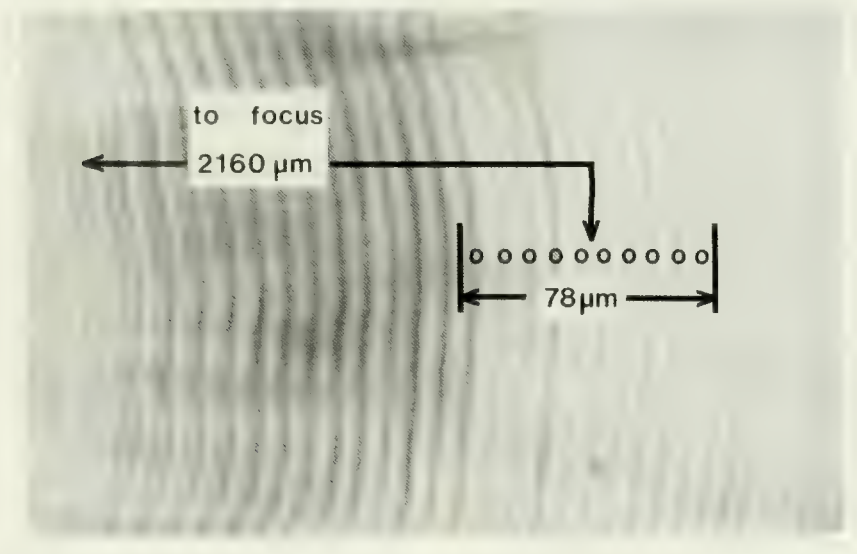

FIGURE 2.—Photomicrograph of a sectioned gindai otolith showing increment microstructure. The 10 daily increments in a short 78 μm segment are enumerated and increment width, i.e., otolith growth rate, is calculated (7.80 μm/d). The distance to the focus is also shown (2,160 μm).

incremental zone with its adjacent discontinuous zone. When counting daily increments, we enumerated the dark discontinuous zones.

From the 94 sectioned otoliths examined for the presence of growth increments (Fig. 2), a total of 852 determinations of otolith growth rate (i.e., increment width) were completed. Note that no increment width data were collected at otolith lengths in excess of 7,500 μm, although otoliths as long as 9,594 μm were measured and used in the regression analysis of log(FL) on log(OL) (see Figure 1). Beyond 7,500 μm (corresponding to 329 mm FL), the pattern of otolith growth became increasingly irregular, and clearly distinguishable daily increments, composed of well-defined incremental and discontinuous zones, were difficult to resolve.

The data show that as otolith length increased the growth rate of the otolith declined (Fig. 3). No detectable difference in the relationship between otolith growth rate and otolith length could be attributed to sex. A partitioned analysis of covariance of the log-transformed data (Table 1) failed to reveal differences in either the slopes or adjusted means of males and females. Thus, data for the two sexes were combined.

The mean growth rate of the otolith $d(\mathrm{OL})/dt_i$

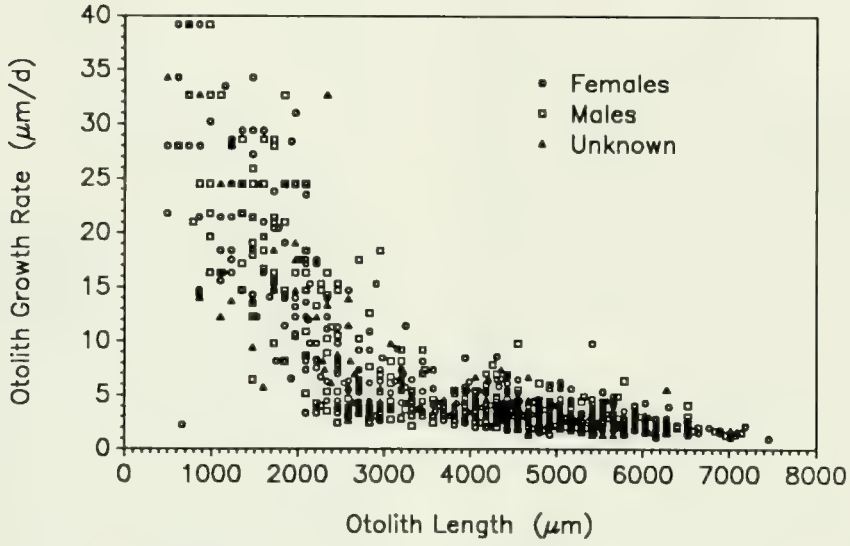

FIGURE 3.—The relationship between otolith growth rate and otolith length plotted for males, females, and specimens of unknown sex.

TABLE 1.—Partioned analysis of covariance of log-transformed otolith growth rate $d(\mathrm{OL})/dt$. Otolith length (OL) was used as the covariate and sex was the treatment variable. The data were divided into two separate linear partitions: data for which OL $\leq$3,700 μm and OL >3,700 μm.

Source	df	Sum of squares	Mean square	F	P
OL $\leq$3,700 μm					
Equality adjusted means	1	0.0015	0.0015	0.01	0.935
Zero slope	1	121.9917	121.9917	551.78	0.001
Error	316	69.8635	0.2219		
Equality slopes	1	0.7158	0.7158	3.26	0.072
Error	315	69.1477	0.2195		
OL >3,700 μm					
Equality adjusted means	1	0.1334	0.1334	1.14	0.286
Zero slope	1	15.9656	15.9656	136.72	0.001
Error	389	45.4273	0.1168		
Equality slopes	1	0.2202	0.2202	1.89	0.170
Error	388	45.2071	0.1165		

and the variance in growth rate σ^2_i within each of the i = 1,15 intervals of otolith length (Table 2) show that as otolith length increased both $d(\mathrm{OL})/dt$ and σ^2 declined. The estimated age (in years) at the point of transition between each of the 15 otolith length intervals (i.e., upon completion of growth through interval k) was

$$\mathrm{Age}_k = \frac{1}{365} \sum_{i=1}^{k} \frac{\Delta(\mathrm{OL})}{d(\mathrm{OL})/dt_i},$$

where Δ(OL) is 500 μm in the application presented here.

Otolith length upon completion of growth through interval k was converted to the equivalent FL (see Figure 1), and the data fitted to the von Bertalanffy growth equation. Because this model poorly represents growth during the early life history, only data representing otolith length intervals in excess of 3,000 μm (i.e., ages >0.8 year) were used in the regression analysis (see Discussion). Table 2 also provides a statistical weight for each of the age estimates. Weighting was desirable because 1) the sample size of each mean varied, 2) the σ^2_i were heterogeneous (proportional to the square of the mean), and 3) compounding of error occurred because of the additive property of the estimator. Weights were calculated as the reciprocal of the sum of standard errors of the means through interval k. The weighted least squares fit to the von Bertalanffy equation (Fig. 4) was

$$\mathrm{FL} = 442\,(1 - \exp(-0.234\,(\mathrm{Age} + 0.892))),$$

with 99.99% of the total variation in FL explained by the model, and with asymptotic standard errors for L_∞, K, and t_0 equal to 14.85 mm, 0.0180 yr^{-1}, and 0.078 year, respectively.

The results of the Monte Carlo simulation indicate that the estimation procedure was unbiased. Following 50 computer replications of the same sampling procedures outlined above, there was no detectable bias in the estimation of either K or L_∞, even though the coefficients of variation for the standard errors of these statistics were both small (0.64 and 0.34%, respectively). Moreover, variance estimates derived from the approximately normal simulation sampling distributions of K and L_∞ provided a basis for placing confidence intervals on the point estimates as follows: $P(0.213 < K < 0.255) = 0.95$ and $P(421 < L_\infty < 463) = 0.95$.

Annual Marks on the Otoliths

On occasion, hyaline and opaque zones were evident in the sagittae of gindai (Fig. 5). These were most easily viewed with light reflected off otoliths immersed lateral side up in water. Typically, however, the zonations were poorly developed or absent entirely. Nonetheless, of the 440 otoliths examined, some banding was evident in 171 (39%), and it was possible to classify the margins of these as either hyaline or opaque. The seasonal expression of hyaline or opaque zones on the margins of these otoliths shows what appears to be an annual periodicity; otoliths sampled during the November–December bimonthly period were characterized almost exclusively by the presence of hyaline margins (94%). Just 2 months later (January–February), only 13% of the otolith samples were similarly classified (Fig. 6). Thereafter, the percentage of otoliths with hyaline margins was never elevated, at least through the

TABLE 2.—Summary statistics of otolith growth by 500 μm intervals in otolith length.

Otolith length interval	Lower bound	Upper bound	N	Mean growth rate (μm/d)	Variance growth rate	Interval duration (d)	Age (yr)	Statistical weight
1	1	500	3	28.03	39.20	17.84	0.0	0.0696
2	501	1,000	30	27.89	90.28	17.93	0.1	0.0164
3	1,001	1,500	55	21.53	42.81	23.22	0.2	0.0132
4	1,501	2,000	60	18.43	41.68	27.14	0.2	0.0118
5	2,001	2,500	83	10.94	32.57	45.70	0.4	0.0115
6	2,501	3,000	71	5.97	12.76	83.68	0.6	0.0115
7	3,001	3,500	54	5.52	4.41	90.55	0.8	0.0114
8	3,501	4,000	49	3.99	1.61	125.25	1.2	0.0113
9	4,001	4,500	110	3.98	2.18	125.54	1.5	0.0113
10	4,501	5,000	99	3.36	1.72	149.02	1.9	0.0113
11	5,001	5,500	95	3.01	1.55	165.98	2.4	0.0112
12	5,501	6,000	78	2.87	1.03	174.03	2.9	0.0112
13	6,001	6,500	39	2.29	0.74	217.91	3.5	0.0112
14	6,501	7,000	18	2.03	0.45	246.60	4.1	0.0112
15	7,001	7,500	7	1.51	0.16	330.97	5.0	0.0111

FIGURE 4.—Von Bertalanffy growth curve for gindai developed from the study of daily growth increments.

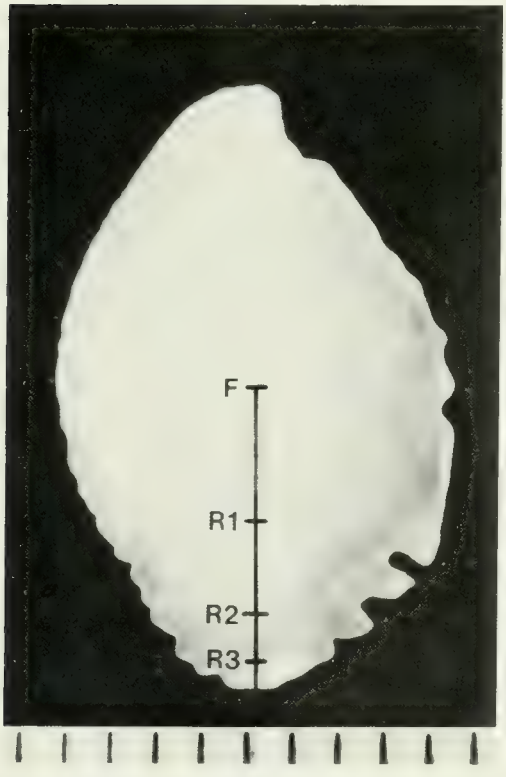

FIGURE 5.—Photomicrograph of a whole gindai sagitta showing the development of hyaline and opaque zones and distance measurements from the focus (F) to the otolith margin and each ring group.

end of August. No data were available for the months of September and October. These results indicate that the markings observed were annular and that the opaque zone first began to form during January–February.

Given the apparent annual periodicity of the markings, growth was estimated by examining their spatial pattern within the otolith. Table 3 presents mean otolith radii measured to the start of each new opaque zone, summarized by sampled age groups, for the 29 specimens that showed well-developed markings throughout their sagittae (e.g., Fig. 5). The table also presents the weighted mean radii converted to estimated FL's by using the regression developed earlier (Fig. 1).

The assembled data were then used to estimate

TABLE 3.—Back-calculated lengths based on annual markings in gindai otoliths. All measurements were taken along the focus to postrostrum growth axis.

		Mean otolith radius (μm) at annulus				
Age group	*N*	I	II	III	IV	V
I	0	—				
II	0	—	—			
III	6	3,233	4,700	5,600		
IV	13	3,054	4,400	5,408	6,315	
V	10	3,130	4,440	5,610	6,530	7,260
Weighted mean (μm)		3,117	4,476	5,517	6,409	7,260
Standard deviation		222	349	427	468	443
Fork length (mm)		128	189	237	278	318

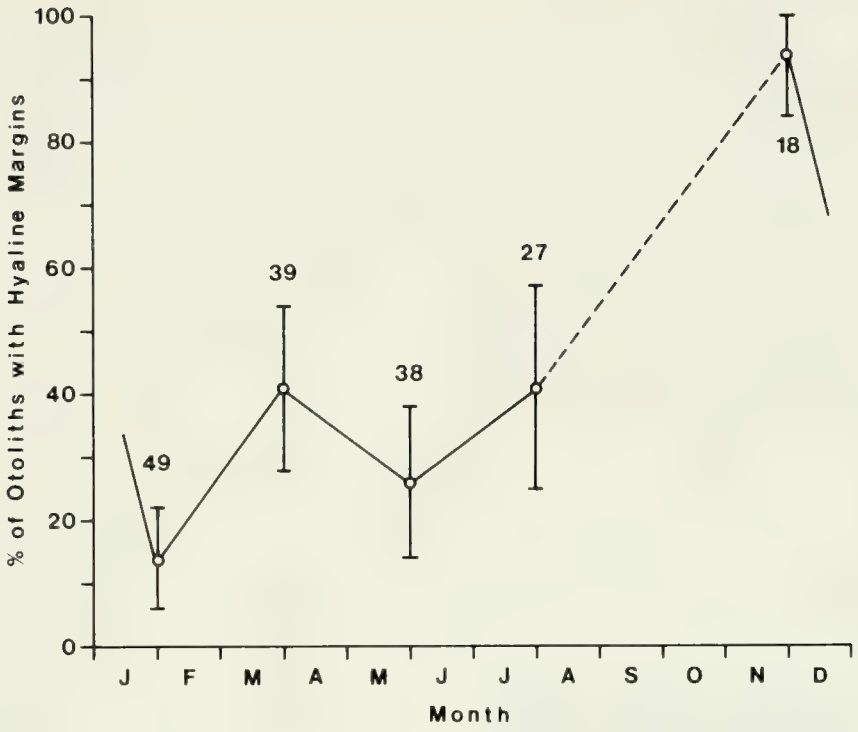

FIGURE 6.—The seasonal occurrence of hyaline and opaque markings on the margins of gindai otoliths.

parameters of the von Bertalanffy growth equation by means of a Walford plot (Ricker 1975), wherein results from a regression of FL at time $t + 1$ against FL at time t provide the basis for estimates of $K = 0.156\ \text{yr}^{-1}$ and $L_\infty = 537$ mm FL.

Length-Frequency Analysis

The combined length-frequency distribution for all gindai sampled (Fig. 7) shows that the mean size was 368 mm FL (standard deviation = 43.1 mm). Fish ranged in size from 190 to 490 mm FL and the modal size was 380 mm FL. Thus, $\ell_{c,\min}$ was estimated to be 385 mm FL. There is evidence to show that, above this size, fish were equally vulnerable to the gear (Ralston 1982, unpubl. data), although smaller individuals were almost certainly underrepresented in the catch because of the selective sampling action of the fish hooks. As $\ell_{c,i}$ increased from 385 to 485 mm FL, the corresponding value of $\bar{\ell}_i$ increased (Table 4). Due to a sample size of one, estimates of the variance and standard error of the mean could not be calculated when $\ell_{c,i} = 485$ mm. Without a statistical weight, the point was excluded from the analysis.

The regression of $\bar{\ell}_i$ on $\ell_{c,i}$ (Fig. 8) was highly significant ($P << 0.0001$), although there was an increasing lack of fit as $\ell_{c,i}$ increased, especially beyond 435 mm FL. This result was due to the diminished statistical weights accorded these points (Table 4). Estimates of the slope and intercept of the regression were $\delta = 0.7051$ and $\xi = 137.31$, with standard errors of 0.0200 and 8.138, respectively. Thus, the mortality to growth ratio (Z/K) is esti-

TABLE 4.—Length-frequency data fitted to the Wetherall et al. (1987) regression model for estimating Z/K and L_∞ (fork length in mm).

Class fork length	N	$\ell_{c,i}$	$\bar{\ell}_i$	Variance	Standard error	Relative statistical weight
390	362	385	409.5	284.4	0.438	22.82
400	314	395	415.9	212.1	0.435	22.94
410	301	405	422.1	157.3	0.441	22.65
420	214	415	429.3	110.7	0.469	21.32
430	165	425	436.3	79.4	0.523	19.10
440	83	435	444.6	62.1	0.705	14.18
450	30	445	453.8	58.3	1.178	8.49
460	10	455	463.3	78.7	2.562	3.90
470	1	465	480.0	200.0	10.000	1.00
490	1	485	490.0	—	—	—

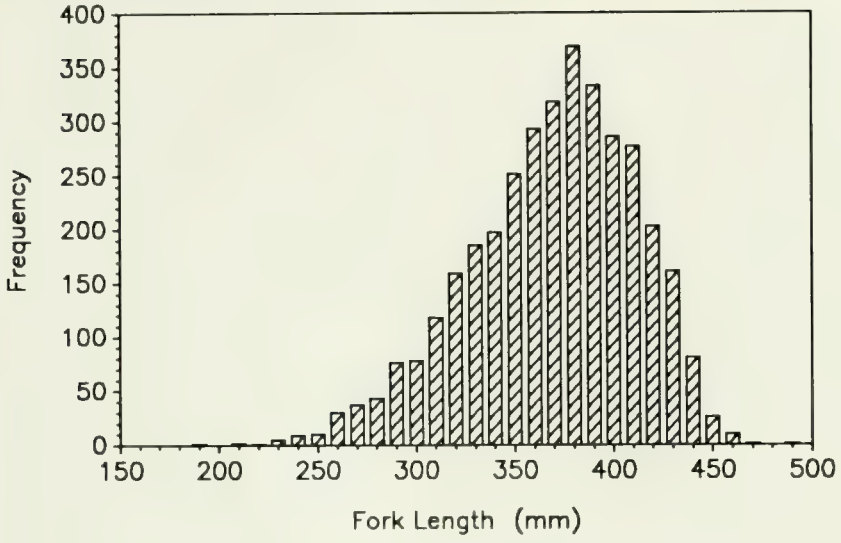

FIGURE 7.—Combined length-frequency distribution for all gindai sampled.

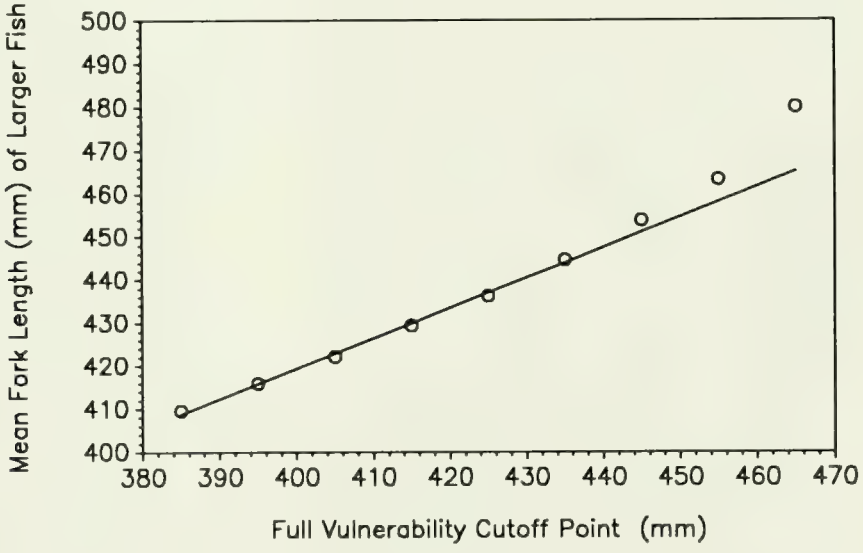

FIGURE 8.—Wetherall et al. (1987) regression of $\bar{\ell}_i$ on $\ell_{c,i}$ (see text for further discussion).

mated to be 2.39 and L_∞ = 466 mm FL. Confidence intervals for these estimates are $P(1.94 < Z/K < 2.62) = 0.95$ and $P(458 < L_\infty < 474) = 0.95$.

With the results presented earlier, it is possible to decompose the Z/K ratio and estimate total mortality rate (Z). For $K = 0.234$ yr^{-1} (increment microstructure), $Z = 0.56$ yr^{-1}, and for $K = 0.156$ yr^{-1} (annual marks), $Z = 0.37$ yr^{-1}.

Spawning Season

Gonadosomatic indexes for male and female gindai are summarized by month of capture in Figure 9. The relative size of gindai ovaries was considerably greater than the testes. More importantly, there was a distinct seasonal trend in the monthly mean gonadosomatic indexes of females, which

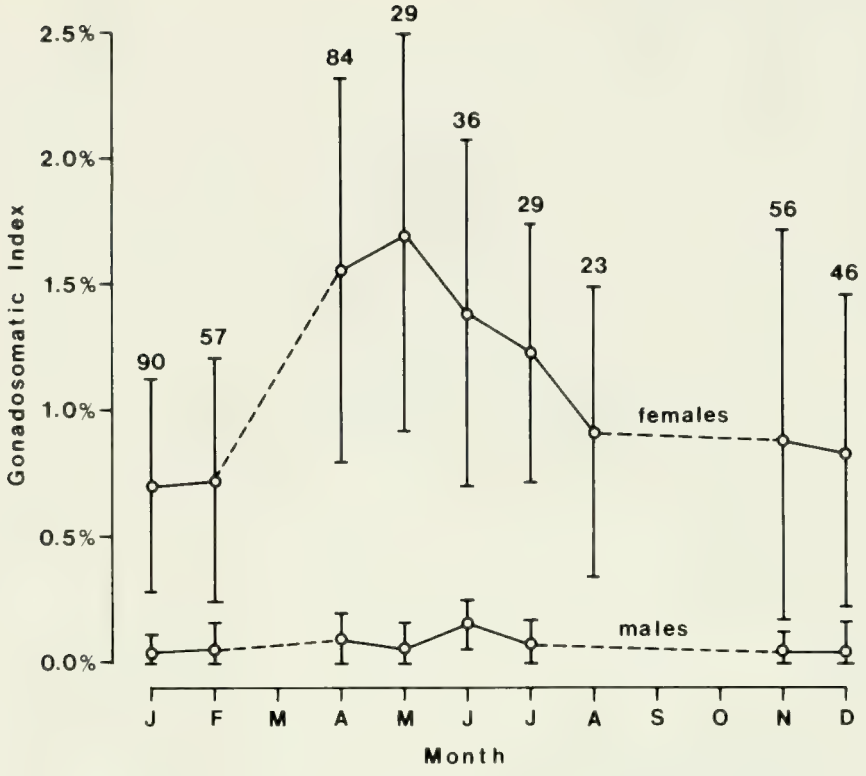

FIGURE 9.—The seasonal pattern of variation in mean gonadosomatic indexes of male and female gindai in the Mariana Archipelago. Note that mean index values are bracketed by sample standard deviations with the sample sizes given above.

reached a peak in May and diminished as the summer progressed.

The same pattern was mirrored in the percentage of ovaries classified to stages IV–VI (i.e., advanced developing to ripe). During the January–March quarter, only 1.4% of the ovaries sampled were so classified. This statistic rose to 48.3% during the April–June period, but then dropped to 19.2% in the July–September quarter and to 16.7% over the last quarter of the year (October–December). The similarity of these two patterns reinforces the interpretation of reproductive seasonality based on gonadosomatic indexes alone (but see deVlaming et al. 1982), and when taken together, these data indicate that peak spawning of gindai in the Mariana Archipelago occurs in late May and early June.

DISCUSSION

Other researchers also have measured the width of daily increments to study fish growth. Methot (1981) used the widths of the outermost three increments in the otoliths of *Engraulis mordax* and *Stenobrachius leucopsarus* as a measure of recent somatic growth rate. Brothers and McFarland (1981) measured the thickness of daily increments in newly recruited *Haemulon flavolineatum* to discriminate life history transitions, as did Gutiérrez and Morales-Nin (1986) in their study of *Dicentrarchus labrax*. Moreover, integration of increment width data to estimate age has been reported, both analytically for *Pristipomoides filamentosus* (Ralston and Miyamoto 1981, 1983) and numerically for *Merluccius angustimanus*, *Merluccius* sp., *Engraulis mordax*, and *Pristipomoides auricilla* (Brothers et al. 1976; Methot 1983; Ralston 1985).

Experimental work has revealed some of the factors that affect the width of daily growth increments. For example, decreased somatic growth in *Oncorhynchus tshawytscha* due to reduced temperature also results in reduced increment thickness (Neilson and Geen 1985). There is conflicting evidence, however, regarding the effect of food ration on daily increment width. Volk et al. (1984) experi-

mentally altered somatic growth rates of *O. keta* juveniles with different experimental feeding regimes and showed a direct linear effect on the mean width of daily increments. Similarly, Marshall and Parker (1982) presented data showing an increase in the relative size of otoliths of starved *O. keta* compared with that of fed controls, even though starvation had no effect on the number of increments. In contrast, Neilson and Geen (1985) found no effect due to ration alone on the thickness of increments in fry of *O. tshawytscha*, although an interactive effect due to ration level and water temperature was shown. These authors also found that increased feeding frequency significantly reduced mean increment width. Lastly, Campana (1984) found that increments of larval (<10 days old) *Porichthys notatus* were more irregularly spaced than in juveniles, as were the increments of fish exposed to a constant photoperiod environment. From these results, it is apparent that the effect of food ration on the width of daily increments is complex and is at present not well understood.

There is still some question concerning how close the coupling is between somatic and otolith growth rates (Brothers 1981; Bradford and Geen 1987). Over the entire lifespan, otolith length and FL typically are highly correlated (Templeman and Squires 1956; Blacker 1974). This situation could not arise were not the growth rates correlated over a similar scale. Still, in the most rigorous examination of the extent of rate coupling to date, Bradford and Geen (1987) found no correlation between the observed growth rates of individual *O. tshawytscha* fry and otolith increment widths over relatively short-term (7–15 d) intervals, although a good correlation over a 51 d interval was observed. These authors point to the relatively conservative character of otolith growth (Casselman 1983; Gutiérrez and Morales-Nin 1986) as the reason for short-term uncouplings between somatic and otolith growth rates.

In our study, otolith microstructure typical of daily increments was observed in the sagittae of gindai (Fig. 2). Daily growth increments were previously described and illustrated for congeneric species by Ralston and Miyamoto (1981, 1983), Brouard et al. (1984), and Radtke (1987). Likewise, we observed annual hyaline and opaque zonations, which have been reported in the hard parts (otoliths and vertebrae) of other lutjanids (Loubens 1978; Chen et al. 1984; Edwards 1985; Manooch 1987; Samuel et al. 1987). Still, of the 11 deep slope species (*Pristipomoides zonatus, P. auricilla, P. filamentosus, P. sieboldii, P. flavipinnis, Aphareus rutilans, Etelis coruscans, E. carbunculus, Lutjanus kasmira, Caranx lugubris*, and *Selar crumenophthalmus*) caught during the Marianas survey and whose otoliths were examined in some detail (Ralston and Williams 1988), only gindai displayed hyaline and opaque zonations, even though all species exhibited microstructure typical of daily growth increments. The absence of annuli in the otoliths of these other species is difficult to explain because many are congeners, most are confamilials, and all but one (*S. crumenophthalmus*) occupy the same general deep-water habitat where gindai are found. As a group, these fishes are exposed to virtually identical environmental conditions. Neither is the diet of gindai in the Marianas particularly distinctive (Parrish 1987).

In contrast to the situation in the Marianas, studies by Loubens (1978) in New Caledonia and Samuel et al. (1987) in the Persian Gulf document distinctive hyaline and opaque annuli in a wide variety of the taxa indigenous to these areas. Although the occurence of annuli in the otoliths of a variety of tropical and subtropical species is now well documented (Manooch 1987), our understanding of when and how they form is quite limited (see below).

Von Bertalanffy growth curves were developed for gindai by using both increment microstructure (Fig. 4) and annual marks. Likewise, the L_∞ parameter of the von Bertalanffy growth equation was estimated by using the regression method of Wetherall et al. (1987). Moreover, the analysis based on annual markings was tentatively validated with an abbreviated form of marginal increment analysis, wherein the seasonal presence or absence of opaque margins was established for the various pooled ring groups. A preferred approach is to measure the marginal increment for each ring group separately (e.g., Chen et al. 1984; Matheson et al. 1986). Although the importance of this type of validation has been overlooked (e.g., Beamish and McFarlane 1983), it is a very useful technique, especially in situations where capture is fatal.

A comparison of von Bertalanffy parameter estimates obtained by the three wholly independent approaches (increment microstructure, annuli, and length-frequency analysis) shows reasonable correspondence. The two estimates of growth coefficient (K) differed somewhat (0.234 versus 0.156 yr^{-1}), although estimates of L_∞ were substantially closer (442, 537, and 466 mm FL, respectively). Given that the annual marks were only weakly expressed, these findings support the conclusion that the microstructure observed in gindai otoliths (Fig. 2) results from the daily accretion of increments and, to the extent

that annuli have been validated (Fig. 6), verifies the method of increment widths employed here. Likewise, the Monte Carlo simulation demonstrated that from an analytical point of view the method is free of significant bias.

The results obtained here were also compared to what we know of lutjanid growth by using the growth performance index developed by Munro and Pauly (1983) (see also Pauly and Munro 1983). For a specifically delimited taxon, this index empirically quantifies the well-known inverse correlation between K and L_∞ (Beverton and Holt 1959; Cushing 1968) and provides a simple basis for predicting K with an estimate of L_∞. Specifically, Manooch (1987) tabulated the results of growth studies covering 46 snapper and 31 grouper (Epinephelinae) stocks and calculated the combined growth performance regression for these taxa ($r^2 = 0.57$). With his equation, we predicted K by using each of our three estimates of L_∞ (see above). These calculations resulted in $K = 0.228$, 0.200, and 0.220 yr^{-1} for maximum sizes derived from daily increment microstructure, annuli, and length-frequency analysis, respectively. The estimates compare favorably with the value obtained solely from the study of otolith microstructure ($K = 0.234$ yr^{-1}), indicating that our results are in close agreement with existing information concerning lutjanid growth.

Calculating the age at first annulus formation provides additional evidence that the approach presented here is valid. The data presented in Table 3 indicate that the first annulus occurs at an otolith length of 3,117 μm. An estimate of age at this otolith length can be obtained from Table 2 by linear interpolation of the data falling in otolith length intervals 6 and 7; i.e., the otolith is 3,000 μm at age 0.6 and is 3,500 μm at age 0.8. This calculation indicates that the first annulus forms at an age of 0.65 year. Given that the opaque zone forms in January–February (Fig. 6), the predicted birth date by back-calculation is early June, in close agreement with observed spawning activity (Fig. 9). Moreover, the mean monthly sea surface temperature at Tanguisson Point, Guam, reaches its annual minimum during January–March (data for the period 1963–72 from Eldredge (1983)), suggesting that temperature fluctuation may be responsible for the formation of the annuli, although this species is found below the thermocline throughout the year (Eldredge 1983) and other closely related sympatric species lack zonations.

Some consideration of the underlying assumptions, advantages, and disadvantages of the method presented here is required. Without doubt, the most important assumption of the approach is that increments are deposited daily throughout the size range where increment width data are gathered. There is a substantial body of literature to show that interruptions to the daily increment record can occur (e.g., Geffen 1982, 1986; McGurk 1984; Jones 1986), especially in larger and older individuals (e.g., Pannella 1971; Ralston and Miyamoto 1983). Likewise, we know that with light microscopy the resolution of increments much less than 1.0 μm in width is physically impossible (Campana and Neilson 1985). This problem therefore becomes increasingly acute among the largest fish (see Table 2 and Figure 3). Together these findings have led to the view that daily growth increments are of little use in ageing large, old fish (Beamish and McFarlane 1987).

In this study, the deposition of daily increments became irregular at otolith lengths in excess of 7,500 μm. Beyond this length, the increments were also difficult to resolve microscopically due to small size. Consequently, no increment width data were collected at otolith lengths >7,500 μm. This corresponds to a FL of 329 mm (Fig. 1), which, although of a size that is reproductively competent (S. Ralston, unpubl. data), is smaller than most of the gindai caught during the field surveys (Fig. 7). Thus, the estimated von Bertalanffy curve presented here is largely based on back-calculated data obtained from the younger stages of growth. Nonetheless, we believe that daily increments can be useful in developing growth curves for use in stock assessments, even if data representing the older stages are not included in the analysis. This is especially true if the L_∞ parameter is estimated from length-frequency data (Fig. 8, Wetherall et al. 1987), avoiding the extrapolation problem described by Hirschhorn (1974). Still, validation of the increment periodicity assumption remains an essential component for future applications of the method.

Another assumption implicitly made is that no systematic bias was introduced into the estimation procedure by the manner in which sampling locations were chosen for measuring increment widths. For example, readings were made at specific points along the postrostral growth axis, i.e., where it was possible to distinguish the characteristic bipartite structure of daily increments. However, we also observed broad transition areas lacking in visually conspicuous microstructural features. If these ill-defined regions were elicited by periods of either fast or slow growth, then our estimates of mean otolith growth rate would be biased. To counter this we tried to representatively sample all daily increments (large and small) and we avoided measure-

ments beyond 7,500 μm (see above). Still, we must assume that otolith growth rates calculated from regions where daily increments are visible are otherwise no different from regions where they are not.

Numerical integration of otolith growth rates provided a series of ordered pairs of age and otolith length. Otolith lengths were then converted to FL through regression analysis. The only FL data included in the nonlinear von Bertalanffy regression (Fig. 4), however, were based on otolith lengths in excess of 3,000 μm. Note that the excluded data (intervals 1–6) represent the first year's growth, i.e., the early life history. Although the von Bertalanffy growth equation has historically been the model of choice in stock-assessment applications, including especially the Beverton and Holt (1957) dynamic pool model, it provides a poor description of growth during the early life history. Inflected growth typically characterizes this stage, which is better fit with a Gompertz-type curve (Zweifel and Lasker 1976). By excluding ages <0.8 years from the von Bertalanffy regression analysis, we constrain the data used to estimate the model to the domain over which meaningful predictions are made. Moreover, predictions of FL based on otolith length are also obtained from regression analysis (Fig. 1). Because the smallest otolith used in developing the regression equation was 5,043 μm (see Figure 1), application of the equation to predict the FL of a fish whose otolith is less than this size represents an unnecessary extrapolation of the fitted model.

One of the side effects of deleting points from the early life history is to diminish the importance of weighting. Note that the statistical weights of the data used in the regression (Table 2) are very similar (coefficient of variation = 0.78%). Thus, although it may be desirable from a theoretical perspective, weighting had a negligible effect on the parameter estimates.

One of the principal advantages recommending this approach is an increase in efficiency and objectivity relative to studies that obtain complete counts of daily growth increments (Uchiyama and Struhsaker 1981; Brouard et al. 1984; Radtke 1987). Because all increments need not be visually conspicuous for a particular preparation to provide useful information, as is true of studies relying on whole counts, the observer can utilize only those portions of the otolith where the microstructure is clearly expressed. Enumeration of ill-defined increments in poorly developed regions of the otolith is avoided. This feature also makes it possible to automate the procedure (Casselman 1983; McGowen et al. 1987) and ultimately to realize the goal of standardizing age determinations (Boehlert and Yoklavich 1984; Boehlert 1985).

Powerful statistical tests of growth heterogeneity also are possible with the acquisition of increment width data (Table 1, Fig. 3). Evaluation of statistical differences in populations with respect to the parameters of the von Bertalanffy growth equation is cumbersome at best (Gallucci and Quinn 1979; Bernard 1981; Kappenman 1981). Analysis of covariance of increment width data provides a convenient and widely available means of testing for growth heterogeneity among any statistical populations of interest.

One of the principal disadvantages of the method outlined here is that growth variation among individuals within the sampled population is lost through averaging of the data. The final growth curve given in Figure 4 describes the mean growth of the sampled population of gindai. Of course, length variation at age is extremely important, and its description is required for application of the more powerful and realistic stock-assessment models, especially in cohort or virtual population analysis (Ricker 1975). Nonetheless, given the difficult conditions surrounding assessment work in tropical environments (Gulland 1982), the application of yield/recruit models is a significant step forward (Munro 1982; Pauly 1982). In conjunction with the analysis of length-frequency distributions, the method proposed here is well suited to help meet that need.

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AGE AND GROWTH OF RED DRUM, *SCIAENOPS OCELLATUS*, FROM OFFSHORE WATERS OF THE NORTHERN GULF OF MEXICO[1]

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A. LOUISE STANLEY[2]

ABSTRACT

Otolith (sagitta) sections are used to accurately age red drum, *Sciaenops ocellatus*, from the offshore northern Gulf of Mexico. Marginal increment analysis indicated that annuli were formed during winter and spring months.

Ages of offshore schooling red drum ranged from 1 to 37 years. Age distributions indicated variability in relative abundances of year classes, with the majority of fish sampled being over 10 years of age. Male and female age distributions did not differ significantly.

Growth differed significantly between males and females. The von Bertalanffy growth equation for males was $L_t = 909(1 - e^{-0.137(t+7.74)})$, and for females was $L_t = 1{,}013(1 - e^{-0.088(t+11.29)})$, where t is age (years) and L_t is fork length (mm).

The red drum, *Sciaenops ocellatus*, is a large sciaenid that inhabits temperate and subtropical nearshore and estuarine waters from Massachusetts to northern Mexico. Juveniles are most abundant in estuarine waters and move from estuarine to nearshore waters as they near maturity (Pearson 1929). The primary spawning stock in the Gulf of Mexico is thought to spawn in nearshore open waters (Overstreet 1983).

The red drum is one of the most popular recreational and commercial fish species in the northern Gulf of Mexico. Recent increase in demand for red drum has escalated the controversy concerning its management; however, little has been reported concerning its growth and population structure.

Age and growth-rate estimates of red drum have only used immature fish from inshore estuarine waters. Pearson (1929) and Wakeman and Ramsey (1985) identified modes in length-frequency distributions and performed scale analysis to determine age estimates. However, Wakeman and Ramsey (1985) reported that scale annuli were unsatisfactory for accurately estimating the age of red drum. Theiling and Loyacano (1976) reported age estimates of red drum from a South Carolina salt marsh impoundment based on otolith examination. Growth rates of juveniles were reported by Roessler (1970), Bass and Avault (1975), and Simmons and Breuer (1962).

No age or growth rate estimates have been published for adult red drum from offshore waters. Accurate information on the age and growth of adult red drum is necessary for determining population dynamics and monitoring the population's response to fishing pressure. Due to the reduction in growth rate in larger individuals, which leads to size overlap between age classes, age estimation by cohort analysis is not feasible. Otolith sections have provided valid age estimates for many large, long-lived fish species (Beamish and McFarlane 1987).

The purposes of this study were to determine if otoliths (sagittae) could be used to obtain valid age estimates for red drum and to estimate growth rates and determine the age structure of the oceanic schooling population of red drum.

MATERIALS AND METHODS

Red drum (1,726 fish) were collected in Texas, Louisiana, Mississippi, and Alabama offshore coastal waters of the northern Gulf of Mexico from September 1985 through October 1987 by purse seine (N = 1,428 from 67 sets) (Fig. 1), gill net (N = 134 from 9 sets), and hook and line (N = 164 from 12 dates). Samples captured by unknown gear from February 1985 through June 1987 (N = 96) were included for marginal increment analysis only.

After fish were randomly sampled from landings, they were measured (fork length) and weighed, and their sex was determined. Sex identifications were

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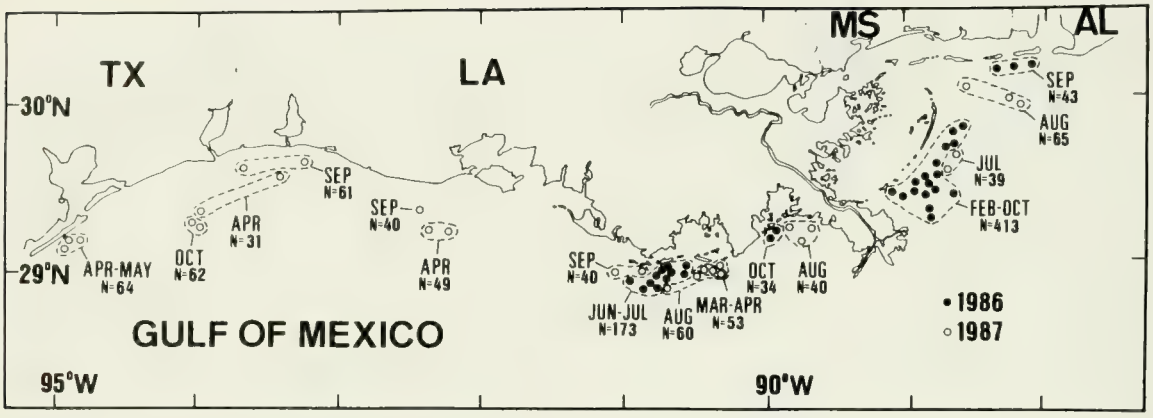


FIGURE 1.—Purse seine sampling locations in the northern Gulf of Mexico. Points represent individual purse seine sets. N's refer to the total numbers of red drum sampled from sets indicated. Precise locations were not available for 6 sets (N = 161).

unavailable for 182 individuals. Sagittae were removed, cleaned, and stored dry for later processing.

Length-weight regressions were fit to the data using the model: weight = a FL^b, where weight = body weight (g) and FL = fork length (mm). Regressions for male and female red drum were compared using analysis of covariance (Ott 1977). A Komolgorov-Smirnov two-sample test (Tate and Clelland 1957) was used to detect possible sampling bias by comparison of length-frequency distributions of fish caught by different sampling gears.

Otoliths were processed for age analysis by embedding them in an epoxy resin (Spurr 1969) and sectioning transversely (0.7 mm thick) through the core of the left sagitta (or the right when the left sagitta was not available), using a Buehler Isomet[3] low-speed saw. Sections were mounted on glass slides with thermoplastic cement (Crystalbond 509 adhesive), sanded on 600 grit wet sandpaper to remove saw marks, polished with alumina micropolish (0.3 μm), and then examined with a compound microscope (transmitted light at 40× magnification). Opaque zones (annuli) were counted in sections from the core to the margin in the medial direction. Appearance of the margin was recorded as either opaque or translucent. If the left sagitta was unreadable, the right sagitta, if available, was prepared and examined. Validation of age estimates was accomplished and the timing of annulus formation determined by plotting percent occurrence of otoliths with opaque margins by month.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Each otolith was aged by two readers, and the resulting age estimates were compared. The coefficient of variation was calculated for age estimates in order to test the reproducibility of age estimates independent of magnitude (Sokal and Rohlf 1981; Chang 1982). If readers' initial age estimates for an otolith did not agree, the section was reread. If the resulting age estimates did not agree, the fish's other sagitta was prepared and read. If the readers did not reach agreement on an age or sections from both otoliths were unreadable, the data for that fish were not used in analyses. All ageing was done without knowledge of the sample source or any previous age estimates.

Year-of-birth was back-calculated from age estimates by subtracting estimated age from the year of capture and assuming that the first annulus formed in winter of year 2 (Beckman et al. in press). Age-frequency distributions were compared using a Komolgorov-Smirnov two-sample test (Tate and Clelland 1957).

Von Bertalanffy (1938, 1957) growth curves were fit separately for males and females by nonlinear regression. The growth equation for length was $L_t = L_\infty [1 - e^{-K(t-t_0)}]$ and for weight was $W_t = W_\infty [1 - e^{-K(t-t_0)}]^3$, where L_t and W_t are the estimated length and weight, L_∞ and W_∞ are the asymptotic length and weight, K is the growth coefficient, t is the age (years), and t_0 is the hypothetical age when length or weight would be zero. A full model, in which separate parameters were fit for males and females, was compared with a reduced model in which sex was not considered. An F-test (Ott 1977) was used to test for differences in the models.

RESULTS

Length-weight regressions for males and females were not significantly different ($P = 0.842$ for intercepts, $P = 0.605$ for slopes). The combined length-weight regression was

$$\text{Weight} = 2.9 \times 10^{-6}\ \text{FL}^{3.22} \quad r^2 = 0.91$$
$$N = 1{,}626.$$

The length-frequency distributions of red drum collected by purse seine (Fig. 2) were significantly different from those obtained by gill net ($P < 0.01$) and hook and line ($P < 0.01$). Therefore, to avoid gear selectivity bias, only purse seine samples were assumed to represent the age-frequency distribution of the offshore spawning population.

Because the sagittae were extremely thick and opaque, they needed to be sectioned before they could be aged. Distinct opaque and translucent growth zones were observed in transverse sections. Annuli were most distinct and the most consistent growth patterns were observed in the region from the core to the proximal surface of the sagitta along the ventral margin of the sulcus acousticus. All counts were made in this region (Fig. 3).

The percentage of sagittae with opaque margins was plotted by month to determine the timing of annulus formation. Opaque zones were deposited in the sagittae during winter and spring months in three successive years of sampling (Fig. 4A). As a consistent pattern of annulus formation was exhibited each year, data were combined for all years in order to compare annulus formation between size groups (Fig. 4B). Data were grouped according to maturity (Overstreet 1983) and growth patterns. Groupings were chosen to include an adequate sample size within each group for analyses as follows: 0–4 annuli — immature and early maturity, rapid growth; 5–9 annuli — mature, rapid growth; 10–19 annuli — mature, reduced growth; and 20–36 annuli — maximum ages, reduced growth. A single peak per year in all plots indicates that one annulus was formed each year in all groups. Age in years for red drum was equal to the number of annuli observed in sections of sagittae. Age estimates were obtained

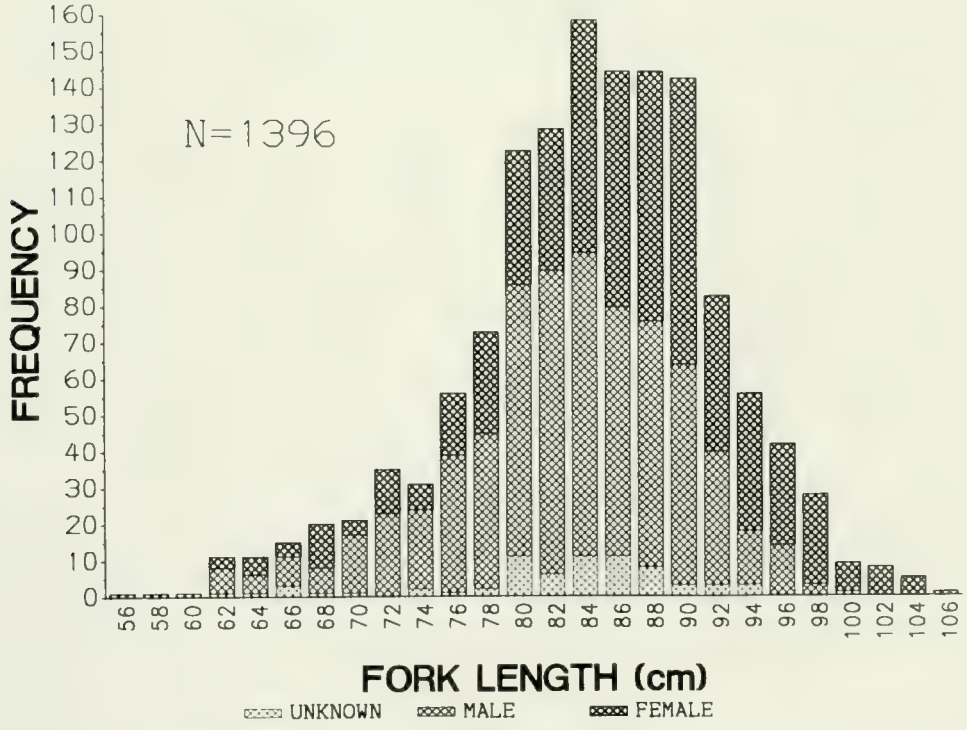


FIGURE 2.—Length-frequency distribution for red drum captured by purse seine from offshore northern Gulf of Mexico waters. "Unknowns" are individuals for which sex identifications were not available.

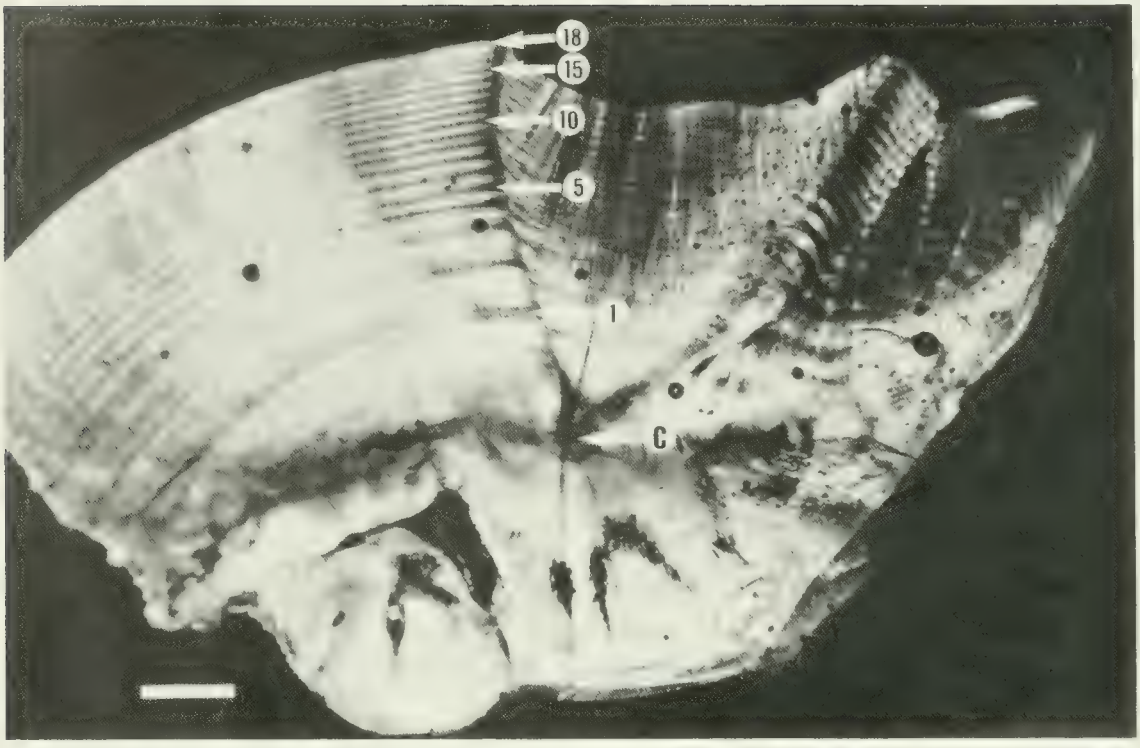


FIGURE 3.—Photomicrograph of a transverse section of red drum otolith (sagitta) sampled in May 1986. Ventral is to the left and proximal is to the top in this figure. "C" indicates the core of the otolith. Numbers indicate annuli in the region where counts were made. There are 18 annuli and an opaque edge. Bar equals 1 mm.

by assuming a birth date of early October (Simons and Breuer 1962; Ditty 1986) and annulus formation beginning the winter of the second year.

Of the 1,726 fish processed, only 94 (5.4%) otoliths were judged unreadable by at least one reader. Of the 58 companion otoliths available from the unreadable fish, only one was judged unreadable. No data were obtained from 36 fish with the first otolith unreadable because their second otoliths were not available. Age estimates, agreed exactly between readers in 95.9% of the samples, were within one year for 99.8% and within two years for 100%. The coefficient of variation for age estimates (V) was 0.0058. Exact agreement was improved to 99.5% by recounting sections for which agreement was not initially reached. Readers differed by one year for the remaining 0.5% of samples, and these differences were resolved for all but one sample (not included in analyses) by counting a section of the other sagitta.

The oldest female red drum was 36 years (995 mm FL, 11.96 kg) and the oldest male was 37 years (940 mm FL, 10.49 kg), both captured by hook and line. Ages of offshore schooling red drum captured by purse seine ranged from 1 to 34 years for females and from 2 to 34 years for males.

There were no significant differences between male and female age distributions in samples taken by purse seine ($P > 0.20$). Age distributions were grouped by year of capture (October through September for 1985–86 and 1986–87) and compared (Fig. 5). Sufficient samples were not available for 1984–85 for comparisons. The 11–14 year age classes dominated the 1985–86 samples and 12–15 year old fish dominated in 1986–87. There was an apparent coherence between the age-frequency distributions for the two sample years. Anomalies in the age distribution for 1985–86 lagged one year behind corresponding anomalies for 1986–87. Age distributions differed significantly between the two sample years ($P < 0.01$); however, there were no significant differences between year of birth distributions between sample years ($P > 0.20$). Therefore, samples were combined for all years to obtain year-

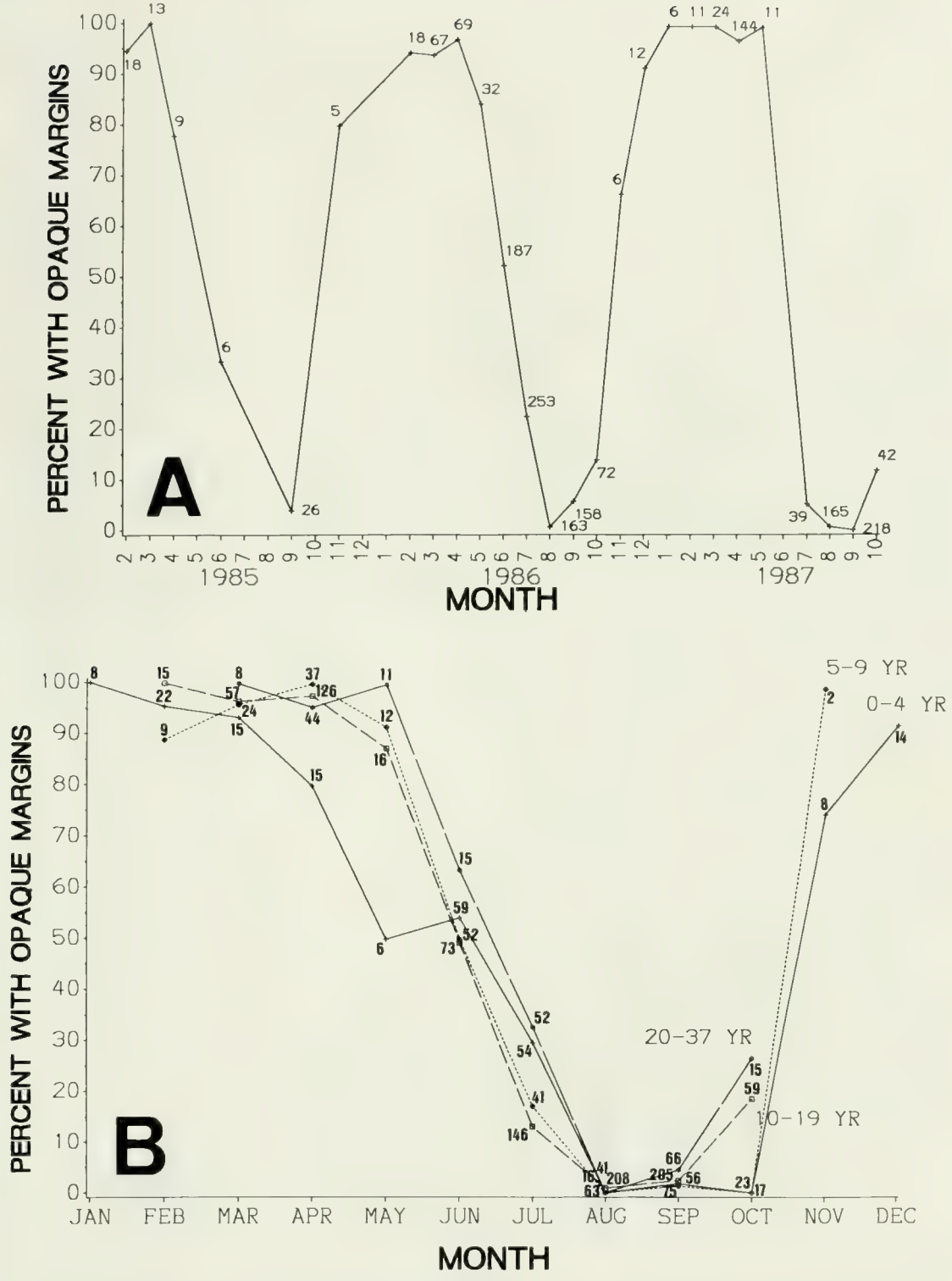


FIGURE 4.—Plot of percent occurrence of otoliths (sagittae) with opaque margins vs. month of capture for red drum A) by sample month and year and B) grouped by annulus counts, sample years combined. Sample size is indicated next to points.

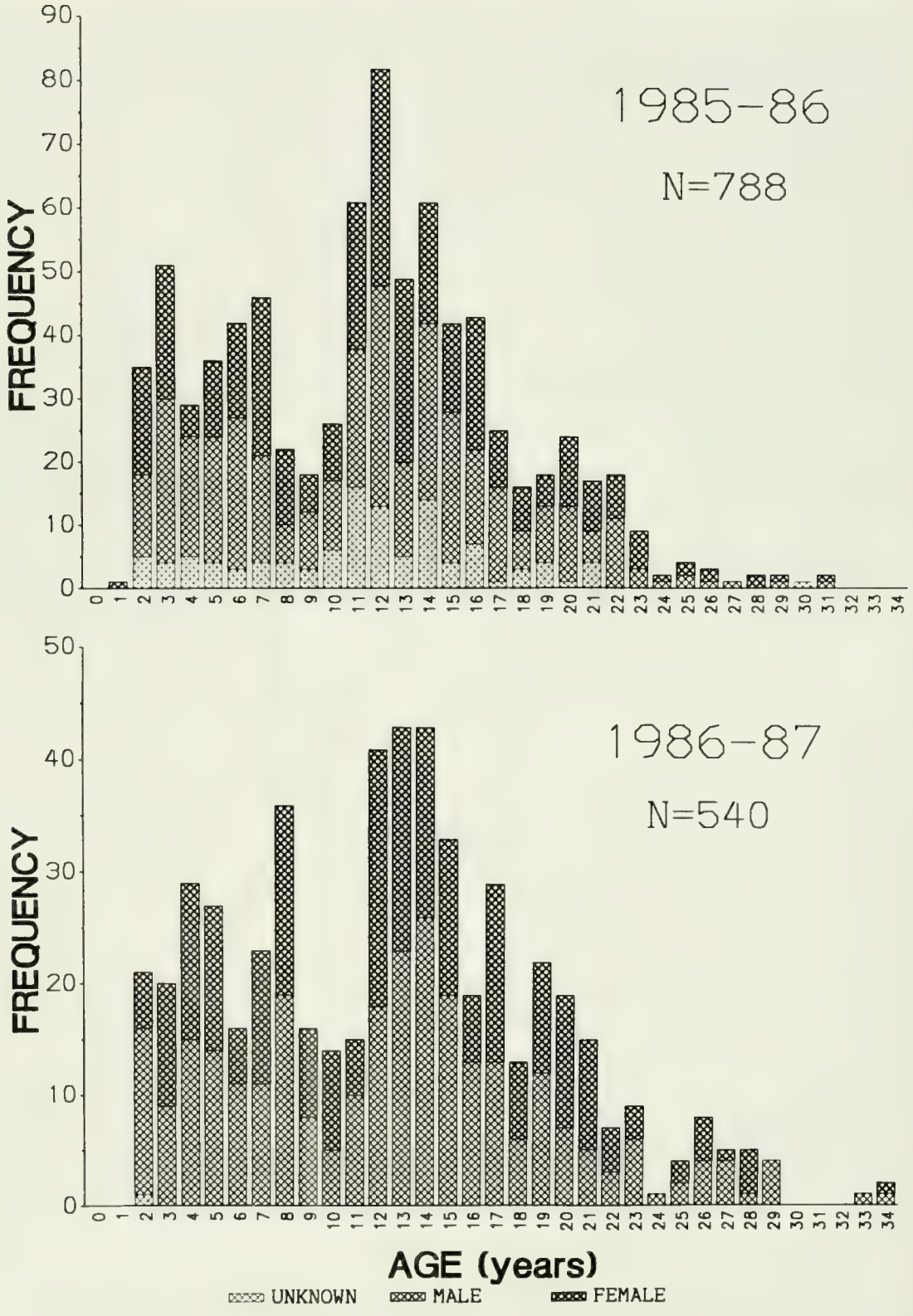

1985–86
N=788
1986–87
N=540
FREQUENCY
AGE (years)
UNKNOWN
MALE
FEMALE

FIGURE 5.—Age-frequency distributions for red drum captured October 1985–September 1986 and October 1986–September 1987 by purse seine from offshore northern Gulf of Mexico waters.

of-birth distributions (Fig. 6). Variability in year-class success is suggested by differences in relative numbers of individuals between year classes.

The separation of sexes in growth models resulted in a significantly better fit by weight ($P < 0.001$) and length ($P < 0.001$) when compared with models in which sexes were combined. Separate von Bertalanffy growth curves best described changes in length (Fig. 7A) and weight (Fig. 7B) of red drum. Equations by length were

$$\text{males:} \quad L_t = 909(1 - e^{-0.137(t+7.74)})$$

$$\text{females:} \quad L_t = 1{,}013(1 - e^{-0.088(t+11.29)})$$

and by weight:

$$\text{males:} \quad W_t = 10{,}548(1 - e^{-0.117(t+8.69)})^3.$$

$$\text{females:} \quad W_t = 15{,}207(1 - e^{-0.079(t+11.57)})^3.$$

DISCUSSION

Sampling

Comparison of length-frequency distribution between gear types demonstrated that gill net and hook and line were different from purse seine collections. Therefore, to provide a basis for documenting and comparing age structure in the offshore schooling population only purse seine collections were used. We assumed that purse seine samples would result in the smallest size selection bias (Nielson and Johnson 1983). We assumed that temporal and spatial bias was minimized because sets were made throughout the year and

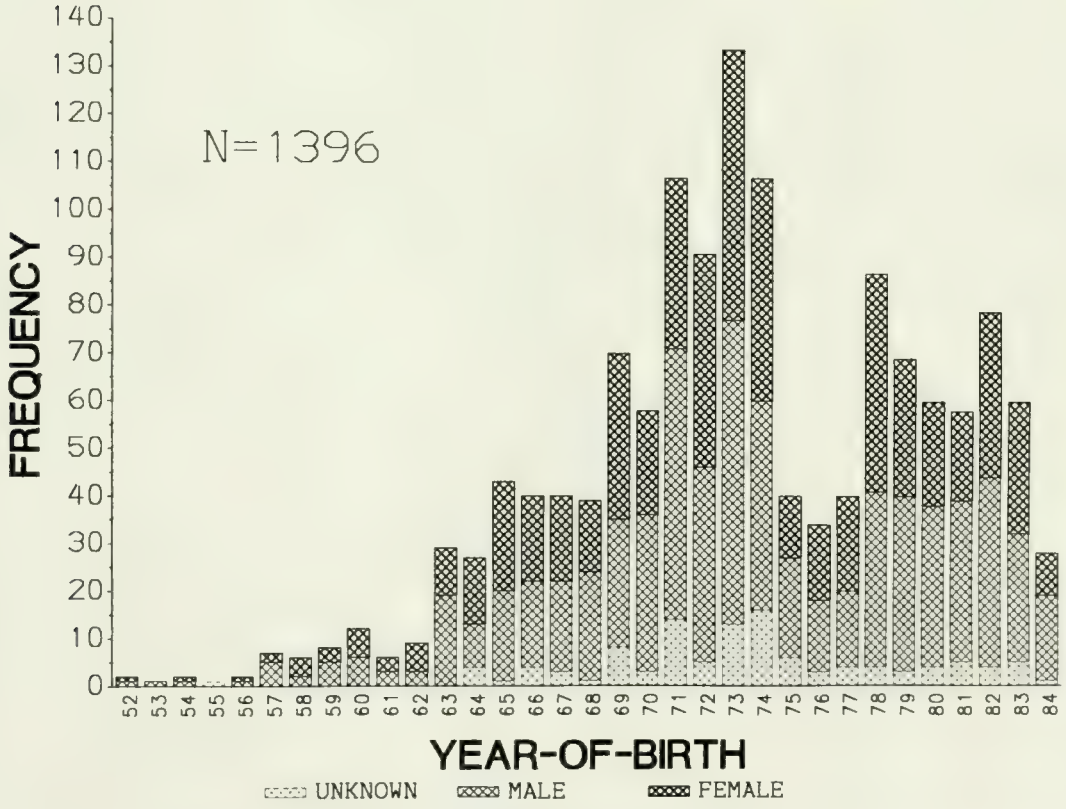
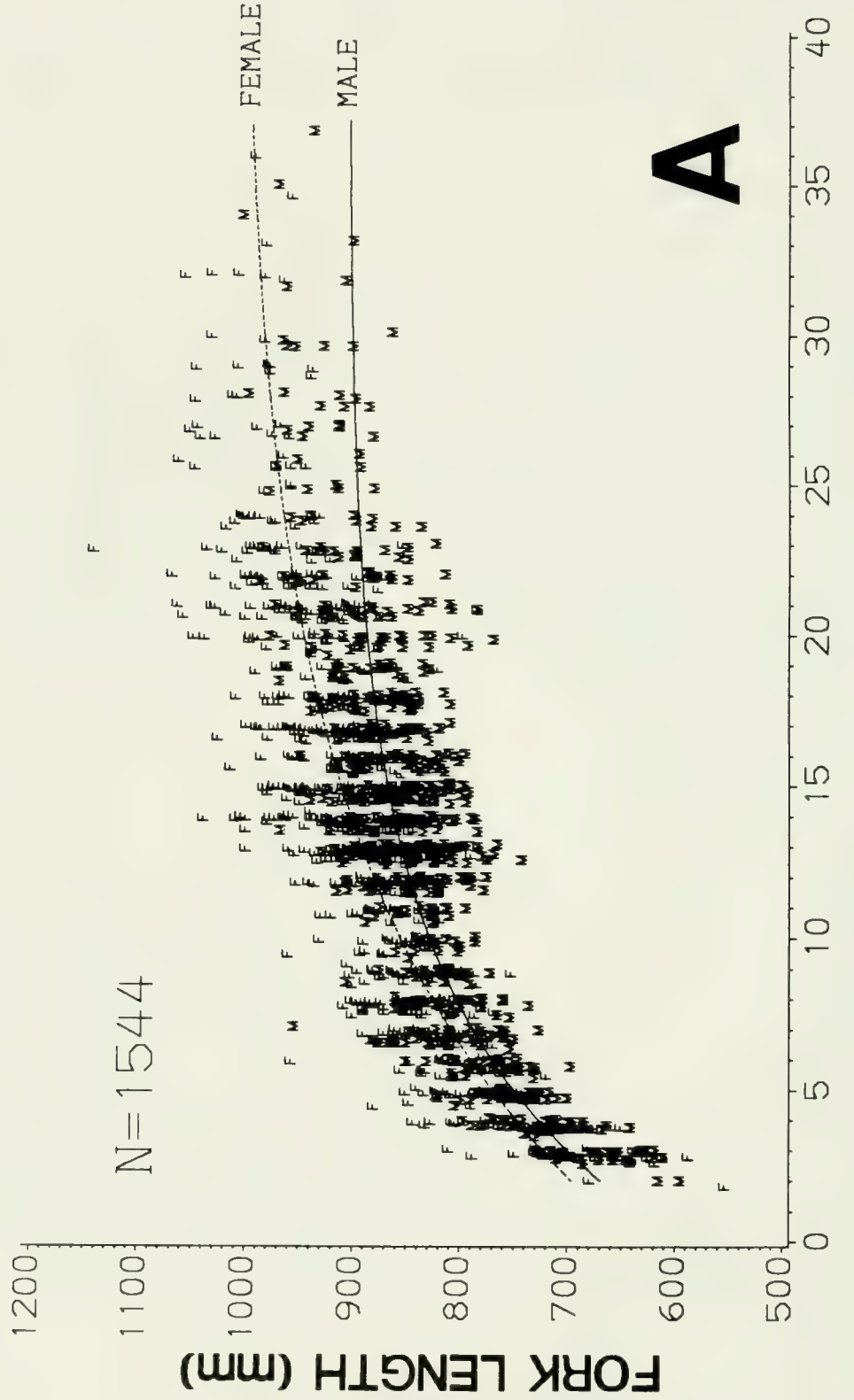


FIGURE 6.—Year-of-birth frequency distributions for red drum captured by purse seine from offshore northern Gulf of Mexico waters, September 1985–October 1987.


FEMALE
MALE
A
N=1544
FORK LENGTH (mm)
AGE (years)
1200
1100
1000
900
800
700
600
500
0
5
10
15
20
25
30
35
40

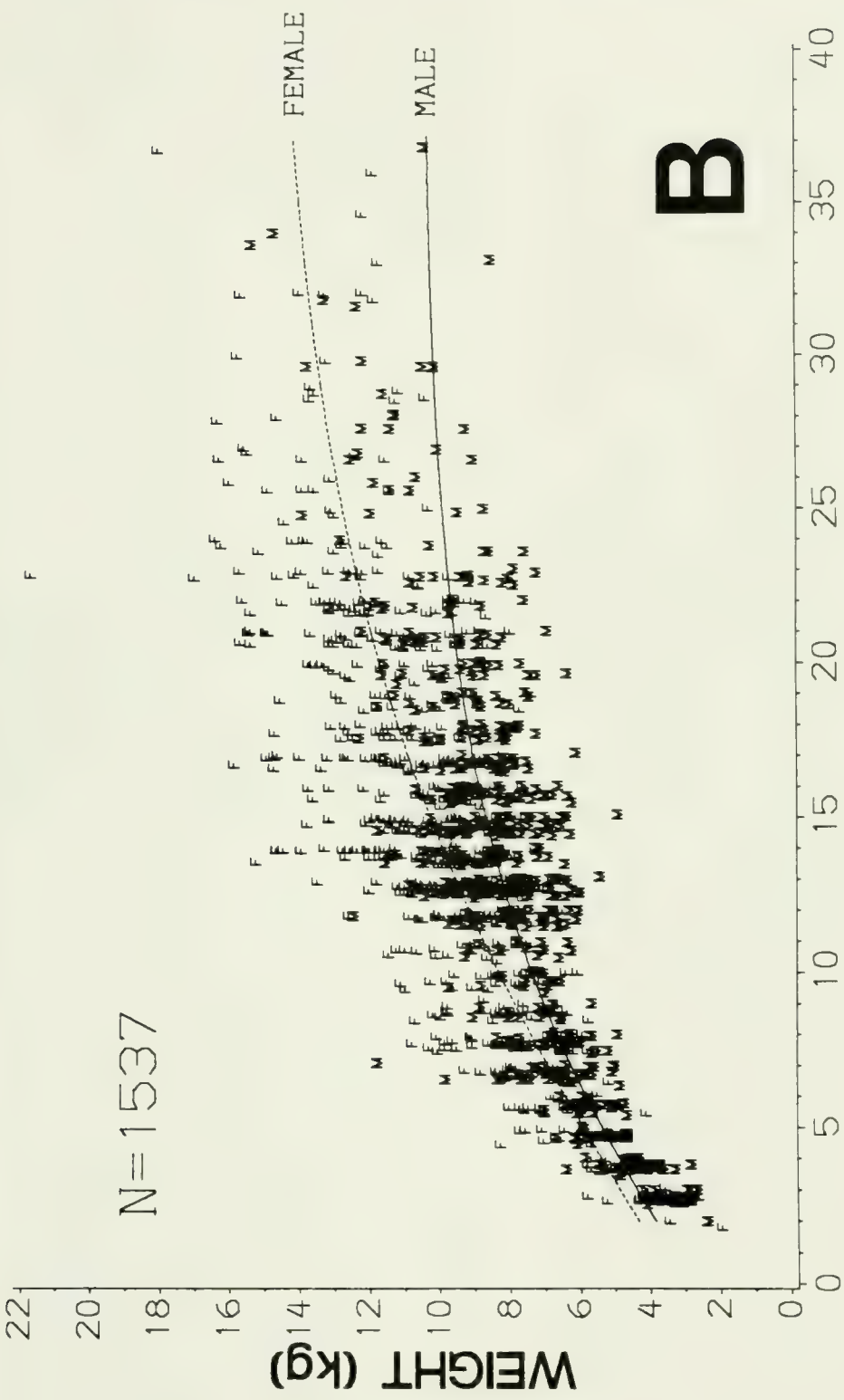


FIGURE 7.—Growth models for male (M) and female (F) red drum captured in offshore northern Gulf of Mexico waters by A) length and B) weight.

across the coastline of the north-central Gulf of Mexico.

Validation

Periodicity of formation of ageing structures must be confirmed over all year classes to validate the use of that hardpart for ageing (Beamish and McFarlane 1983). Beckman et al. (in press) validated that the first two annuli were formed yearly in sagittae of immature red drum from estuarine waters. The use of marginal increment analysis in this study validated that annuli continued to be deposited in red drum sagittae once per year in fish up to 37 years old. There was no significant variability in timing of annulus formation with stage of maturity or with change in growth rates with age.

Precise, reproducible age estimates were obtained for red drum using transverse sections of sagittae. Almost 100% agreement between two readers was achieved by recounting otoliths or counting the fish's other sagitta when age estimates disagreed. Initial disagreements were usually resolved by recounting the otolith, suggesting initial miscounts or errors were due to recording and transcription. Unreadable otoliths were primarily those with inadequate sample preparation. Discarding difficult-to-age otoliths, which are often from older fish, could bias age distributions as well as von Bertalanffy growth parameters (Hirschhorn 1974). Recounting otoliths for which age estimates did not initially agree and utilizing both sagittae to obtain a readable sample allowed us to minimize the number of unused sections.

The same seasonal pattern of annulus formation reported in this study was observed in sagittae of red drum in inshore estuaries (Beckman et al. in press). This pattern is also similar to that observed in another sciaenid, the Atlantic croaker (Barger 1985). The formation of an opaque zone in red drum sagittae in winter and spring months may correspond to reduced growth rate during this period (Doerzbacher et al. 1988). In West African sciaenids an opaque zone was formed apparently in response to cold temperatures (Poinsard and Troadec 1966).

Growth

The von Bertalanffy growth coefficients for other sciaenids (e.g., Barger 1985; Wakeman and Ramsey 1985, cited by Pauly 1980) were generally greater than those obtained for red drum in this study. Growth parameters reported herein differ from those obtained by Wakeman and Ramsey (1985) for red drum; however, their model was based only on young fish from inshore waters that have higher growth rates (Beckman et al. in press). The growth models reported in this study were derived primarily from mature slower growing fish. The negative values of t_0 predicted suggests that our models do not adequately describe growth of young fish unrepresented in our data. Separate models may be necessary to describe growth of immature red drum from inshore waters (Richard Condrey pers. commun.[4]). The large variation in size at age beyond year 5 makes it impossible to precisely predict age of red drum using length or weight.

Our estimates of maximum red drum age are greater than those previously suggested. Pearson (1929), Simmons and Breuer (1962), and Wakeman and Ramsey (1985) used the scale method and reported a maximum age of 5, 3, and 4 years, respectively. The use of validated ageing techniques for red drum from otoliths more accurately estimates their ages and provides much improved management data bases.

Female red drum attained significantly larger sizes than did males, with growth curves diverging with increasing age and maturity. Larger size in females has been postulated as a life history strategy in fish for increasing reproductive potential through increased egg production capability (Roff 1983). The similarities in age-class compositions between sexes indicated that the increased female size was attained through somewhat higher growth rates and not greater longevity.

Age Structure

Examination of the age composition of the offshore population revealed that red drum begin to appear in the offshore population as early as year 2. Their appearance offshore coincides with their absence inshore by four or five years of age (Pearson 1929; Simmons and Breuer 1962; Wakeman and Ramsey 1985). The 1973 year class was the most abundant, and earlier year classes demonstrated a decay pattern indicative of natural mortality. The year classes since 1973 were variable and could be interpreted variously to indicate several poor year classes, high mortality, or incomplete recruitment to offshore schooling populations, assuming no bias in the sampling procedures. Inadequate data are available to determine which are primary factors affecting age distributions.

[4]Richard Condry, Coastal Fisheries Institute, Louisiana State University, Baton Rouge, LA 70803, pers. commun. January 1988.

Comparison of age distributions between years provided two estimates of the population age-class structure, varying in time and areas sampled. The similarities in year-of-birth distributions in 1985–86 and 1986–87 suggest that the same population was sampled in both years and that distributions may reflect the true offshore schooling population of red drum, assuming no sampling selectivity. Recruitment into the population from one year to the next was evident only in the youngest age classes, possibly due to migration from inshore nursery areas. The relatively low numbers of individuals in age classes of less than 10 or 11 years suggests a possible delay or reduction in recruitment into the schooling population sampled. Other possible factors affecting abundance of younger age classes offshore are fishing pressure on inshore red drum, size specific fishing offshore, or other factors affecting survival.

ACKNOWLEDGMENTS

Sampling efforts were supported by the Louisiana Sea Grant College Program; the U.S. Department of Commerce, NOAA, Marine Fisheries Initiative Program (MARFIN); the Louisiana State University, Coastal Fisheries Institute; the Louisiana Department of Wildlife and Fisheries; and the National Marine Fisheries Service. Sampling involved the cooperation of many recreational and commercial fishermen. We thank Gary Fitzhugh, Bruce Thompson, David Nieland, Robby Parker, David Stanley, and Tony Gaspard for their assistance in data collection and analysis, and James Geaghan for statistical assistance.

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DISTRIBUTION, ADVECTION, AND GROWTH OF LARVAE OF THE SOUTHERN TEMPERATE GADOID, *MACRURONUS NOVAEZELANDIAE* (TELEOSTEI: MERLUCCIIDAE), IN AUSTRALIAN COASTAL WATERS

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ABSTRACT

Ichthyoplankton surveys in southern Australian coastal waters indicate that larvae of the temperate gadoid, *Macruronus novaezelandiae*, differed consistently in mean size and age between sample sites. These observations are consistent with the hypothesis that larvae are being passively advected by longshore currents from a spawning area on the west coast of Tasmania to habitats along the southeastern and eastern coasts. The ages of larvae at specific points along the advection route vary, which suggests there is considerable variation in rate of larval transport. Rates of larval growth increased exponentially for at least the first 50 days of planktonic life, though the slope of the growth curve varies both between years and between seasons. Growth rates also differ between sampling sites: early stage larvae (≤15 d postfirst-feeding) grew more rapidly at sites close to the spawning area, whereas older larvae (≥25 d postfirst-feeding) grew more rapidly the farther they were from the spawning area. Migration of *M. novaezelandiae* to a specific spawning area and the subsequent transport of larvae away from this area appears to be an adaptive response by the population to, on the one hand, regional differences in conditions for larval growth and, on the other, changing needs of the larvae at different stages of their development.

Planktonic eggs and larvae of marine fishes are subject to dispersion (= diffusion) and advection (= transport or drift), topics of considerable theoretical and empirical interest to larval fish ecologists (Smith 1973; Wiedemann 1973; Talbot 1977; Okubo 1980; Naganuma 1982; Power 1986). The causes and consequences of diffusion, aggregation and patchiness of larvae are largely unknown due to problems of sampling at an appropriate scale (Hewitt 1981). Advection of larval fishes, however, has been frequently documented and has been studied in some detail (see Norcross and Shaw 1984). Temporal variability in advection can have considerable impact on rates of larval survival (Norcross and Shaw 1984) and has long been suggested to be a major determinant of year-class strength in populations subject to variable current regimes (Walford 1938; Harden Jones 1968; Nelson et al. 1977; Bailey 1981; Parrish et al. 1981). In at least some species, eggs and larvae are placed in currents that transport them to larval and juvenile nursery areas (Parrish et al. 1981). Even within species, however, the extent of adult migration and larval countermigration varies widely between populations, presumably in response to local hydrographic conditions (Cushing 1986). Eastern North Atlantic gadoid stocks, for example, provide some of the classic examples of adult migration to spawning grounds and subsequent passive drift of larvae to nursery areas (Harden Jones 1968); in contrast, larvae of at least some Western Atlantic stocks of the same species develop entirely in the immediate vicinity of the spawning grounds (O'Boyle et al. 1984, Sherman et al. 1984; Smith and Morse 1985).

By comparison with their Northern Hemisphere relatives, little is known about the reproduction and larval ecology of southern temperate gadoids, despite the fact that several constitute major fisheries. One species, the blue grenadier or hoki, *Macruronus novaezelandiae*, supports such a fishery in Australia and New Zealand, with combined annual landings of approximately 100,000 t (tonnes). Available data indicate that both the New Zealand and Australian populations migrate each winter to discrete spawning areas, located, respectively, on the west coasts of the New Zealand South Island

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(Bladodyorov and Nosov 1978[4]; Patchell 1982; Kuo and Tanaka 1984a, b) and Tasmania (Wilson 1981, 1982). These migrations imply a countermigration by either larvae or juveniles back to adult habitats (e.g., Harden Jones 1968; McKeown 1984). Patchell (1982) reported movement of eggs away from spawning areas in New Zealand, and subsequently collected juveniles in coastal habitats hundreds of km from the spawning area. Similarly small juvenile *M. novaezelandiae* have been collected in estuaries and on the coastal shelf along the southeastern and eastern coasts of Tasmania (Wilson 1981, 1982; Last et al. 1983; Bulman and Blaber 1986), over 200 km from the known spawning area.

[4]Bladodyorov, A. I., and E. V. Nosov. 1978. The biological basis of rational exploitation of *Macruronus novaezelandiae*. Unpubl. TINRO manuscr. English translation held by New Zealand Ministry of Agriculture and Fisheries, Fisheries Research Division Library, 7 p.

How juveniles move between the spawning area and these coastal habitats, or even whether this is a rare or common occurrence in the species is unknown. The present study investigated the distribution, sizes, and ages of larval *M. novaezelandiae*, on the basis of which patterns of advection, larval growth, and the relationship between the two could be inferred.

METHODS

Sampling Procedures

Ichthyoplankton samples were collected at approximately two monthly intervals from April 1984 to September 1985. Samples were obtained at fixed stations along nine transects located roughly equidistantly around Tasmania (Fig. 1). Additional samples were obtained in July and August 1985 along

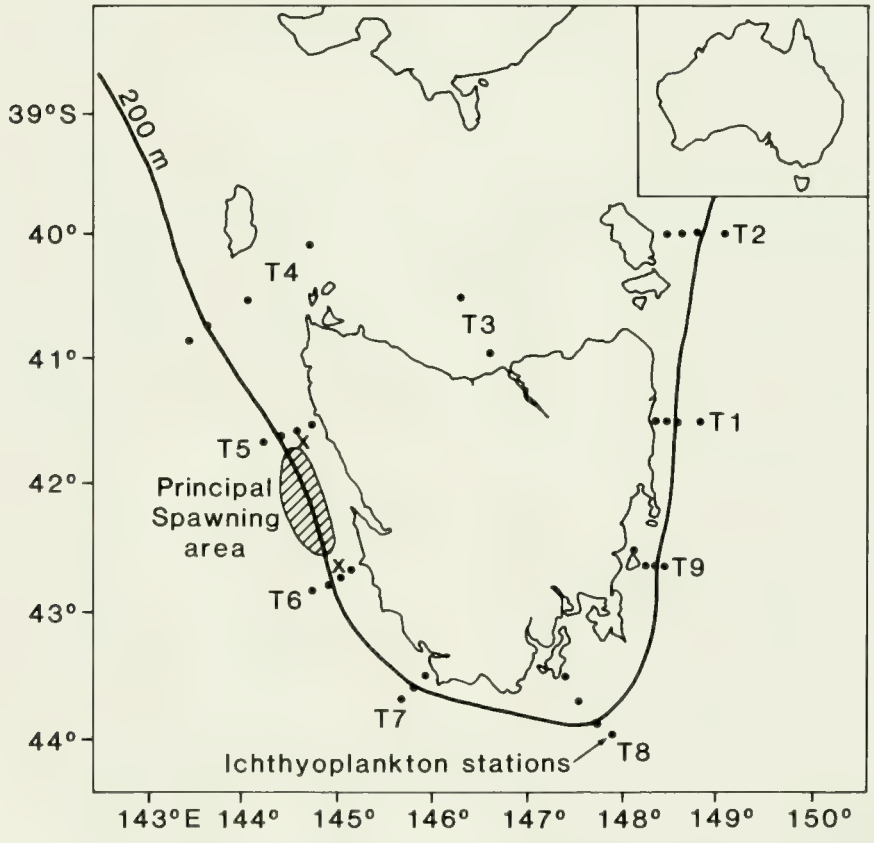

FIGURE 1.—Location of ichthyoplankton sampling sites (solid circles) and release points (X's) of drift cards. The drogued buoy was released at the release point for drift cards south of the spawning area. Cross-hatched area indicates apparent principal spawning area of *Macruronus novaezelandiae* in Australian coastal waters.

the southern coast of mainland Australia (see Figure 3). Transects 1 through 8 consisted of 2–4 stations (4 on average), depending upon the width of the continental shelf. These stations were designated "nearshore" (at a depth of 30–50 m), "midshelf" (70–100 m), "shelf edge" (immediately offshore of the shelf break and usually at a bottom depth of approximately 200 m) and "offshore" (1 nmi offshore of the surface temperature/salinity front between inshore and offshore water masses or, if no front was evident, at 10 nmi offshore from the shelf edge station). In the second year of the study, occasional samples were collected at sites along the west coast between regular transect lines, in order to improve the spatial resolution of analyses and to increase sample sizes.

Two samplers were used: a rectangular midwater trawl (RMT) 1 + 8 (see Baker et al. 1973 for description) and a 1 m diameter ring net fitted with a pivoting bridle system similar to the Tranter-George plankton net (Tranter and George 1972). Mesh sizes for the RMT-8 was 3 mm and 1 mm for the net and cod end, respectively, and 333 μm throughout for the RMT-1. The ring net consisted of 500 μm mesh with a 333 μm cod end. Initially, all sampling was done with the RMT 1 + 8 in a fixed open mode. Because it was difficult to fish the net in rough seas and to calibrate its fishing characteristics (see Pommeranz et al. 1982), the RMT 1 + 8 system was replaced after three cruises (April–August 1984) with the more manageable ring net. The ring net was subsequently used on transects 1 through 8, while the RMT system was retained for study of the vertical distribution of larvae at transect 9.

Each station consisted of a stepped oblique tow made to a maximum depth of 200 m—bottom depth permitting—parallel to bottom contours. The net was fished at 10 m depth steps for three minutes each at a vessel speed of approximately 2 knots. Net depth was monitored continuously by a Simrad[5] trawl eye. The volume of water filtered was calculated using Rigosha B flowmeters, calibrated in a flume tank. Reported catch rates are standardized to numbers per 1,000 m^3 of water filtered. Except where specified below, sampling was not standardized to time of day.

Data on larval depth distributions were obtained with the 1 m ring net off the west coast of Tasmania. Sampling was conducted on 20 and 21 July 1986 between transects 5 and 6, over a bottom depth of 100–120 m. As this site is close to the spawning area of *M. novaezelandiae*, the catches consisted primarily of small larvae. On each tow, the net was sent to depth quickly, allowed to stabilize at the selected depth for 1–2 minutes, and then retrieved slowly on a continuous oblique path. Tows were made in the order of progressively deeper depths. As each tow integrated larval abundance to the maximum depth of the tow, it was assumed that differences in standardized catch rates between adjacent strata reflected larval abundance in the depth range added. Twenty-four tows were made, varying from 15 to 90 minutes and from 10 to 90 m depth. Tows were made in six sets, three during the day (0830–1330) and three at night (2300–0400). Sunrise and sunset were at 0730 and 1700 (Australian Eastern Standard Time), respectively.

Samples were divided by hand into two portions. One portion was fixed in a buffered 3.7% aqueous solution of formaldehyde and the other in 95% ethanol. The former were used to identify larvae; larvae in the ethanol-fixed samples were used for ageing and assessment of growth rates. Larval abundance data are based on both portions for each station. The ages of *M. novaezelandiae* larvae were determined by examination of otolith microstructure, following procedures outlined in Brothers et al. (1976). Whole otoliths were extracted from the larvae and viewed under transmitted light at 720–2500× using a Leitz Orthoplan microscope and high resolution, closed-circuit television (Ikigami Model CTC-6000). Otolith features were measured with a sonic digitizer (Science Accessories Corporation Graf/Bar) supported by an Apple 2e microcomputer and a modified version of the Basic program DISBCAL (Frie 1982). Viewed laterally, the otolith measured (the lapillus) was virtually circular; all measurements reported are to the point on the perimeter farthest from the primordium (i.e., the axis of maximum growth). Rates of larval growth are uncorrected for shrinkage. Preliminary results suggest shrinkage (TL) due to alcohol preservation averages approximately 5% and is only weakly correlated with larval size (regression of percent shrinkage against preshrinkage TL, slope = −0.005, $R^2 = 0.18$, $n = 27$). Shrinkage will affect estimates of absolute growth rates, but the available literature (Theilacker 1980; Fowler and Smith 1983) suggests it should not bias comparisons between growth rates, provided the larvae being compared were collected and fixed in the same manner. Statistical analyses were done using Statview 512+, Vers. 1.1.

[5]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Validation of Ageing Procedures

Larvae of *M. novaezelandiae* were reared in captivity to determine the age at which otoliths form. Fertile eggs were obtained by stripping running ripe males and females immediately after their capture by trawl on the spawning grounds. Eggs were incubated in 1 L plastic jars, which were filled with seawater, and placed in a seawater bath. Initial incubation temperatures ranged from 14° to 18°C (sea-surface temperature was approximately 14°C). Upon return to the laboratory, eggs were transferred to 2 L glass jars and placed in an aquarium maintained at a constant temperature of 14°C (±0.2°C). Incubation jars were not aerated, and no attempt was made to feed the larvae.

Under light microscopy, otoliths were first apparent in *M. novaezelandiae* embryos 10 hours prior to hatching. At hatching, the sagittae and lapilli were developed and conspicuous. The asterisci were first apparent 3–4 days after hatching. Otoliths from newly hatched larvae characteristically have a conspicuous dark and broad band close to their edge, which is apparently laid down at hatching. Scanning electron microscopy indicated the otolith within this hatching mark consisted of a spherical primordium surrounded by an area with little conspicuous structure. The radius of the hatching mark varied between specimens but did not differ significantly between reared larvae ($\bar{x}$ = 6.9 μm, range = 6.7–8.5 μm, n = 17) and wild-caught larvae ($\bar{x}$ = 7.5 μm, range = 5.3–9.7 μm, n = 17) ($P > 0.1$, two tailed t-test).

All wild-caught larvae had a second exceptionally dense and very conspicuous band. The radius of this band varied from 10.2 to 16.4 μm ($\bar{x}$ = 13.2 μm, n = 17), i.e., approximately 5–7 μm outside the hatching mark. Although the otoliths of reared larvae reached sizes close to this (maximum radius = 13.1 μm), this distinctive band was not evident in their otoliths. As the largest of these larvae had fully ossified jaws and well-developed guts and had all but exhausted their yolk reserves, the second major band in the otoliths may have formed close to or coincident with first feeding. The microstructure of the otolith differed markedly inside and outside of the "first-feeding band". Within its radius, there was little evidence of consistent structuring (other than the hatching mark); beyond the first-feeding mark, increments were unambiguous, increasing in width exponentially. As we saw no indication that any structure prior to the first-feeding mark formed daily, otolithic age for the larvae examined is defined as the number of increments external to this feeding mark. This age is used in analysis of growth and advection patterns, unless otherwise indicated.

Based on the observed incubation time (55–60 hours) and the observed time required for reared larvae held under temperature conditions similar to those during the spawning season to develop to a stage where feeding was possible (6 days) (Bruce 1988), the total age of larval blue grenadier can be estimated as otolithic age +6 days, with a probable error of about ±2 days. Hence, date at first-feeding for a particular larva was calculated as date of collection less otolithic age, and date of spawning was date of collection less total age. In general, the development of otolith structure prior to first-feeding of larvae in *M. novaezelandiae* is remarkably similar to that of other gadoids (Radtke and Waiwood 1980; Bolz and Lough 1983; Dale 1984), as is the proposed time frame.

The hypothesis that increments in the otolith are formed daily was tested by following cohorts of individuals and determining whether the change in the number of increments matched the known sampling interval (Campana and Neilson 1985; Jones 1986). Larvae were sampled within 0.5 km of a drogue deployed near the spawning grounds (see description of drogue below). Larvae from three plankton tows made near the onset of a 26 h period (0521–0649) were compared with those from two tows made close to its end (0628–0701). The respective samples were pooled because the number of larvae caught in each tow was small. Mean sampling interval between the first and last set of tows was 24.6 hours (1.025 days). Size-frequency distributions of larvae collected are given in Figure 2A. Modal analysis (means and variances unconstrained) for the first sample set indicated the presence of two normally distributed populations, with means at 3.61 and 4.66 mm SL (SE = 0.06 and 0.05, respectively); analysis of the size-frequency distributions of larvae collected approximately a day later also indicates two means, at 4.12 and 4.91 mm SL (SE = 0.29 and 0.07, respectively). The smaller of these two means is poorly defined statistically, however. Re-analysis with the added constraint that larvae grew at the same rate across the size range of the two means (which is a reasonable approximation for such small larvae—see below and Figure 9) indicated means for the first set of samples at 3.62 and 4.65 mm SL, and for the second at 3.86 (which is within one SE of the unconstrained mean) and 4.89 mm SL, which fitted closely observed distributions. The average difference in larval sizes between the first and second set of samples (i.e., mean growth for the 24.6 h period) was 0.24 mm SL. The number of

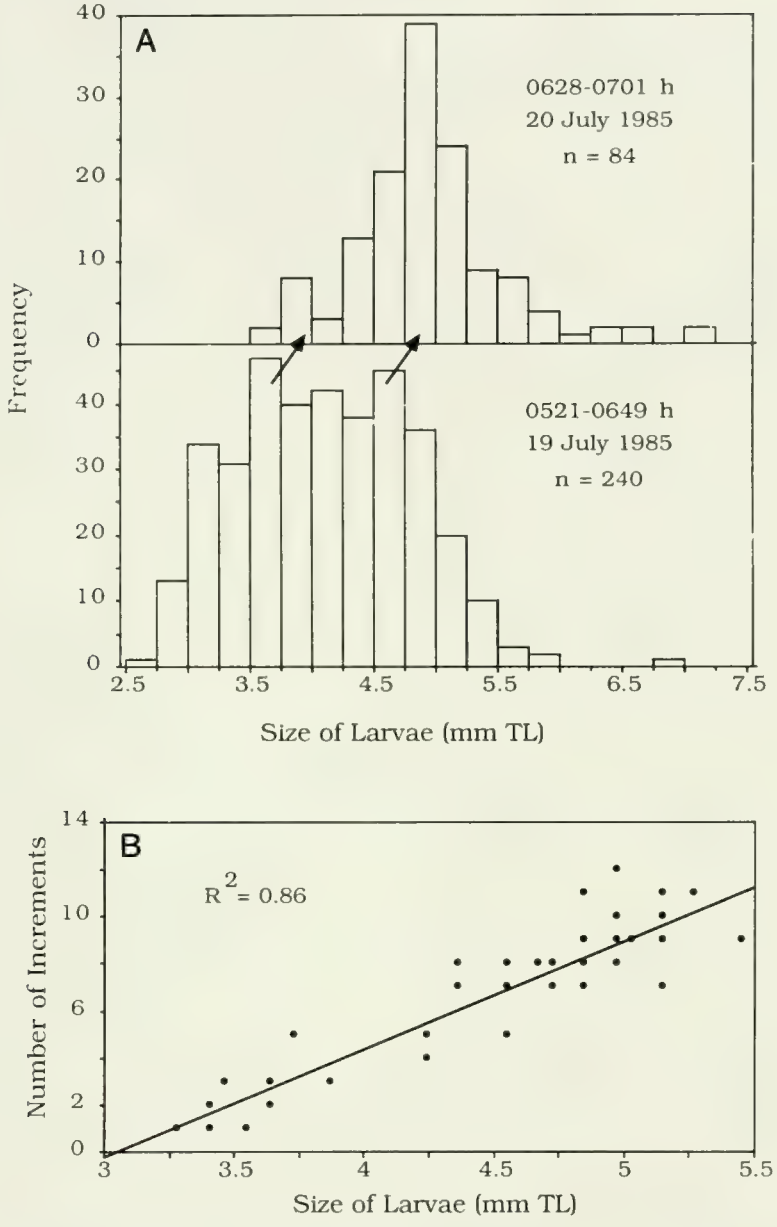

FIGURE 2.—A. Size-frequency distributions of larval *Macruronus novaezelandiae* collected in tows near a drogue at the onset and end of a 26 h sampling period. Arrows indicate apparent progression of the modes. B. Correlation between larval total length and number of postfirst-feeding increments for pooled subsample of larvae drawn from populations in 2A. The correlation is significant at $P << 0.01$ and accounts for 86% of the variance in number of increments.

growth increments in these larvae was estimated by drawing subsamples from both populations, proportional to the number of individuals in each 0.25 mm size class, and regressing increment number against larval size. The relationship is linear and highly significant (Fig. 2B). Based on the least squares regression of increment number on SL, a change in mean larval size of 0.24 mm corresponded

to a change in increment number of 1.102 increments. This compared favorably with the sampling interval, 1.025 days, and is consistent with predictions based on daily increment formation.

Physical Oceanography

Current patterns in the spawning area were investigated in June–August 1985 by 1) release of surface drift cards near the spawning grounds, 2) deployment of a surface drifter drogued at 50 m for 24 hours, and 3) examination of surface isotherms as indicated by a shipboard thermosalinograph.

A total of 2,250 surface drift cards were released during the 1985 spawning season. Cards were released in four lots, two at each of two points (Fig. 1), located immediately north and south of the spawning ground. A set of cards was released at each point on 21 and 22 July and again on 11 and 12 August.

A drifter was deployed at 0800 h on 19 July south of the spawning area at a site at which large numbers of newly hatched larvae were collected (lat. 42°43.4′S, long. 145°04.0′E) (Fig. 1). The drifter consisted a 8.5 m parachute drogue suspended at a depth of 50 m below a large surface buoy fitted

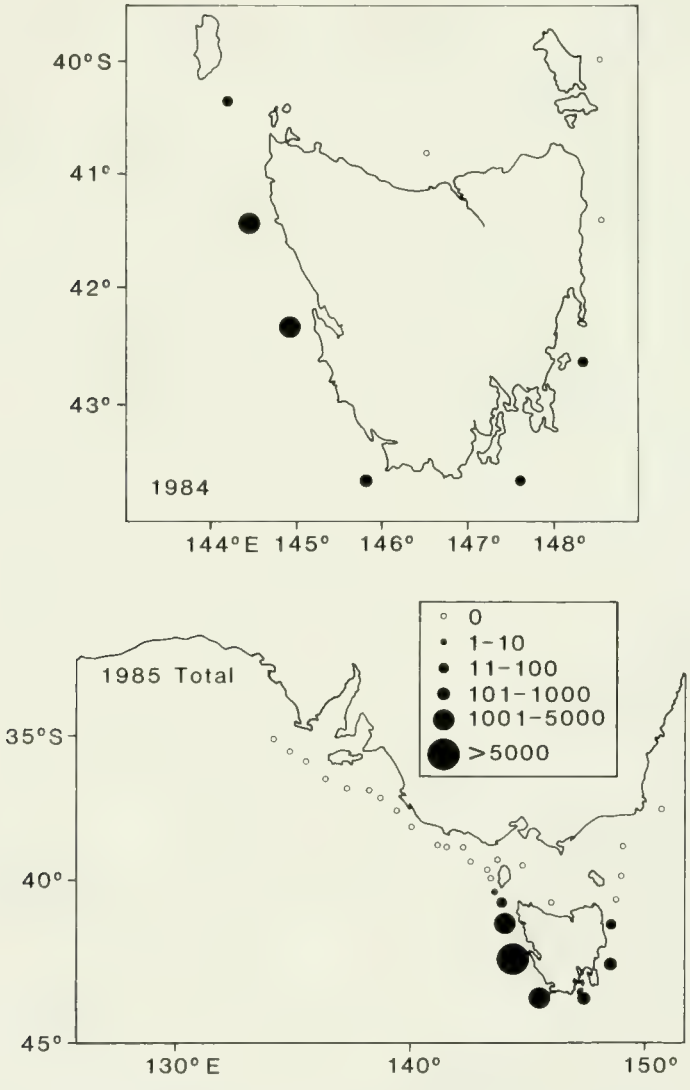

FIGURE 3.—Total catches of larval *Macruronus novaezelandiae*, pooled by transect, for 1984 and 1985, standardized per 1,000 m^3 of water filtered.

with a cross-shaped radar reflector and a flashing light. The buoy's position, determined by radar fixes on coastal features, was recorded at 3 h intervals.

Surface temperature and salinity were recorded continuously during all cruises, using a Grundy thermosalinograph. The readings were calibrated against measurements taken during routine hydrographical sampling using depth-profiled CTD and Niskin bottle casts.

RESULTS

Distribution of Larvae

In both 1984 and 1985, *M. novaezelandiae* larvae were caught almost entirely in the winter, peaking in abundance in July and August, and primarily along the western and southern coasts of Tasmania. The highest densities were caught off the midwest coast (Fig. 3). Larvae were collected in largest numbers at nearshore and midshelf stations (Fig. 4), i.e., at bottom depths of 30–100 m and well inshore of the shelf break, a pattern consistent across all transects.

During depth-stratified sampling, relatively few larvae were caught on tows made at depths ≤20 m (Fig. 5). Samples taken with the ring net suggest that larvae occurred predominantly between 20 m and 90 m (at a maximum depth of 100–120 m) and that the depth of peak abundance was greater at night (60 m and below) than during the day (approximately 40 m). In a two-factor analysis of variance,

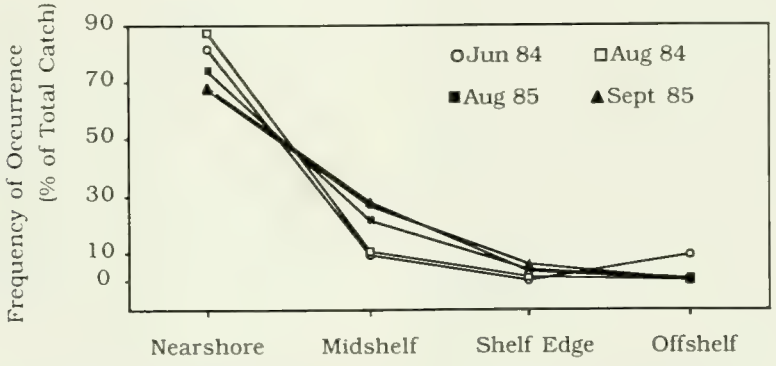

FIGURE 4.—The proportion (percent of total for cruise) of larvae caught on each cruise during the spawning season at each of the four typical sampling positions across the continental shelf.

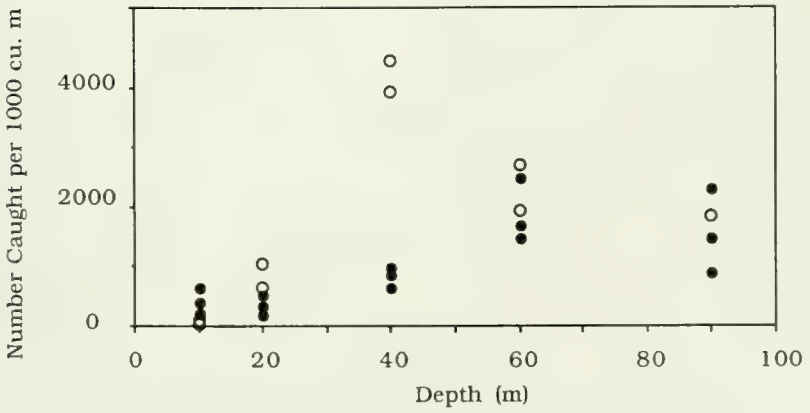

FIGURE 5.—Number of larvae caught during day (open circles) and night (closed circles) periods by oblique tows made to maximum depths ranging from 10 to 90 m. Numbers caught are standardized to 1,000 m^3 of water filtered.

depth, time of day, and the interaction term were all highly significant ($F_{3,16}$ = 22.6, $F_{1,16}$ = 13.5, and $F_{3,16}$ = 9.6, respectively, $P < 0.01$ in all cases). Differences between replicate samples were small, accounting for only 12.7% of the variance, despite the same patch of water not being sampled each time.

Although larvae of *M. novaezelandiae* were collected at stations all along the western, southern, and southeastern coasts of Tasmania, the age and size-frequency distributions of these larvae differed conspicuously between collecting sites. In 1984, larvae younger than 5 d postfirst-feeding were caught only on transects 5 (9% of total) and 6 (91%). This is consistent with earlier suggestions (Wilson 1981, 1982) that the area along or on the continental shelf between Sandy Cape (transect 5) and Cape Sorell (transect 6) is the primary spawning area for *M. novaezelandiae* in Australian coastal waters. The ages of the larvae caught at transect 5 varied widely. From transect 6 south and east along the coast, the ages of larvae collected increased consistently with increasing distance from the spawning area (Fig. 6A). Differences between transects in age distributions of larvae are highly significant ($F_{5,110}$ = 38.8, $P << 0.01$), as is the correlation between age and distance (= number of transects, based on the equal spacing of transects along the coast) from transect 5 (r = 0.64, $P << 0.01$). The latter correlation was also significant for each of the 1984 spawning season cruises individually, except the last one (September), when all larvae collected were relatively old. Differences between transects in the sizes of larvae caught paralleled differences in ages (differences between transects, $F_{5,110}$ = 27.9, $P << 0.01$), with the largest larvae collected farthest along the coast from the spawning area (at transect 9) (cor-

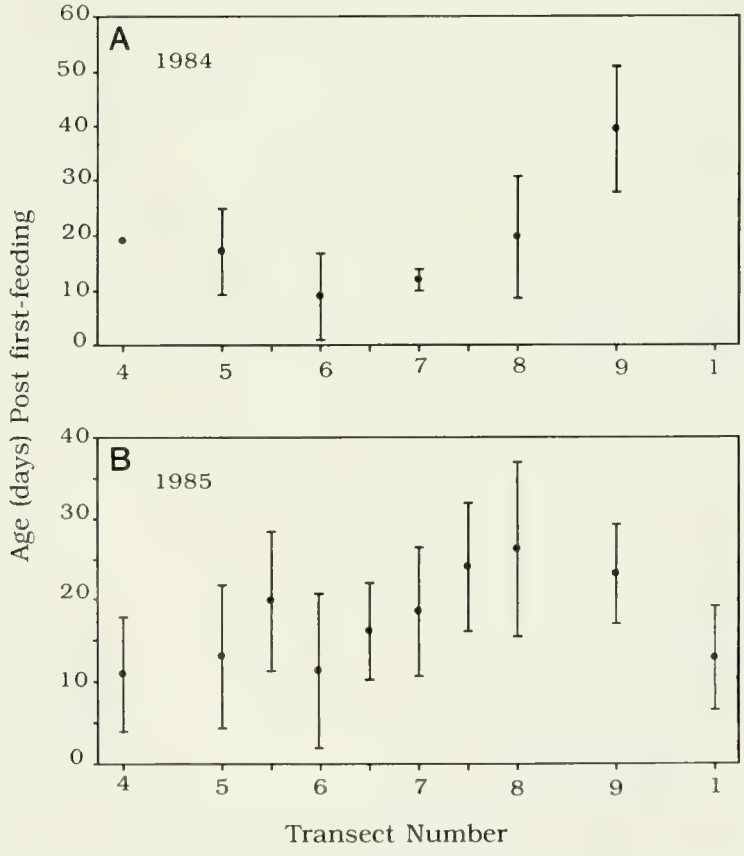

FIGURE 6.—Ages of larvae caught at each transect, pooled across sampling periods, for 1984 and 1985. Vertical bars indicate means ±1 SD; SE are in all cases <3 days. Differences in larval ages across transects are highly significant for both years, as are the correlations between age and distance from transect 5.

relation between distance from transect 5 and size, $r = 0.63$, $P << 0.01$).

The relationships between sampling site and larval ages and sizes in 1985 were similar to those in 1984, though apparently complicated by several factors. As in 1984, differences between transects were highly significant ($F_{9,355} = 14.2$, $P << 0.01$, and $F_{9,355} = 12.38$, $P << 0.01$, for age and size, respectively), as were the correlations between both variables and distance from the midwest coast ($r = 0.33$, $P < 0.01$, and $r = 0.36$, $P < 0.01$, for age and size, respectively) (Fig. 6B). At transects 5 and 6, 95% of larvae aged <5 d postfirst-feeding were caught. However, some larvae <5 d postfirst-feeding were also collected at transects 4 and 7, and a few larvae <15 d postfirst-feeding were found off the northeastern coast of Tasmania (near transect 1). The age of the latter is much less than would be expected based on northward advection from the known spawning area (Gunn et al. in press), which suggests strongly the presence of a second spawning area, involving few adults, of the northeastern coast. The occurrence of these larvae confounds a general relationship between distance from the west coast and the ages and sizes of larvae caught. Hence, although for each cruise in 1985 larvae consistently increased in age and size with increasing distance from transects 5 and 6, there was a broad range of larval ages at each transect, relatively old larvae at several transects, and young larvae on the east coast.

Larval Advection

On the basis of the distribution of larvae of different ages and sizes around Tasmania, we hypothesized that most larvae were being carried passively by a longshore current southwards around the coast from the primary spawning area off the west coast. The drift card returns, the movement of the drogue deployed on the west coast, and the distribution of surface isotherms are generally consistent with this hypothesis.

Most drift card returns were from sites southeast along the coast from the release points, including all of those from the first series (July 1985) (Fig. 7A, B). The drogue, deployed at the southern point at the same time drift cards were released, also drifted longshore and to the south (straight-line distance of 11.8 km in 26 hours). Movement of the drogue was conspicuously related to wind speed and direction, varying from nil at slack winds (<9 km/h) (as measured by shipboard anemometer) to slightly >1 km/h for a 9 h period when wind speed averaged approximately 55 km/h from the northwest (350° magnetic). For the second release series, drift cards returned shortly after being released on 11 August 1985 at the northern site were predominantly from points inshore (east) and slightly north of the release point (Fig. 7C). Of the 43 cards returned from this release, only two were found south of the release point; four, found on mainland Australia, had been transported north more than 150 km. In contrast, southeasterly transport was indicated by the cards released at the southern point on 12 August; only three of 30 returns were from sites north of the release point (Fig. 7D). One of these cards was found on South Arm Beach (southeastern Tasmania) on 27 August 1985. It had drifted slightly over 350 km in 15 days. Additional returns from this release included three cards from New Zealand, one from Flinders Island (northeast of Tasmania), and one from the southeastern coast of mainland Australia. All of these were found several months after being released.

The distribution of surface isotherms also suggests the presence of a southward flowing current along the west coast of Tasmania during the spawning period of *M. novaezelandiae*. In both years of the study, west coast temperature plots in late autumn and early winter were dominated by a tongue of water, 1°–2°C warmer than the surrounding water, that extended southwards along the coast, becoming narrower and cooler to the south (Fig. 8). This tongue of warm water, oriented parallel to the coast, was observed on all winter cruises. Satellite imagery has since documented it to be a regular seasonal feature off the west coast of Tasmania (C. Nilsson, in prep.).

Growth

Otolithic age was determined for 116 larvae in 1984 and 365 larvae in 1985. Growth trajectories (length-at-otolithic age) for *M. novaezelandiae* larvae were log linear for both years (Fig. 9), accounting for 96% of the variance in length at age in 1984 and 84% of the variance in 1985. Residuals exhibit no conspicuous systematic deviation from linearity in either year and no marked increase in variance with age. Hence pooled data indicate consistent exponential growth through at least the first 50 days of larval life, with no indication that the rate of growth declined late in larval life. The slope of the semilog regression was steeper, albeit only slightly, in 1984 than in 1985 (0.043 vs. 0.039, respectively, ANCOVA $F_{1,477} = 2.56$, $P < 0.001$), which suggests that growth was more rapid in 1984.

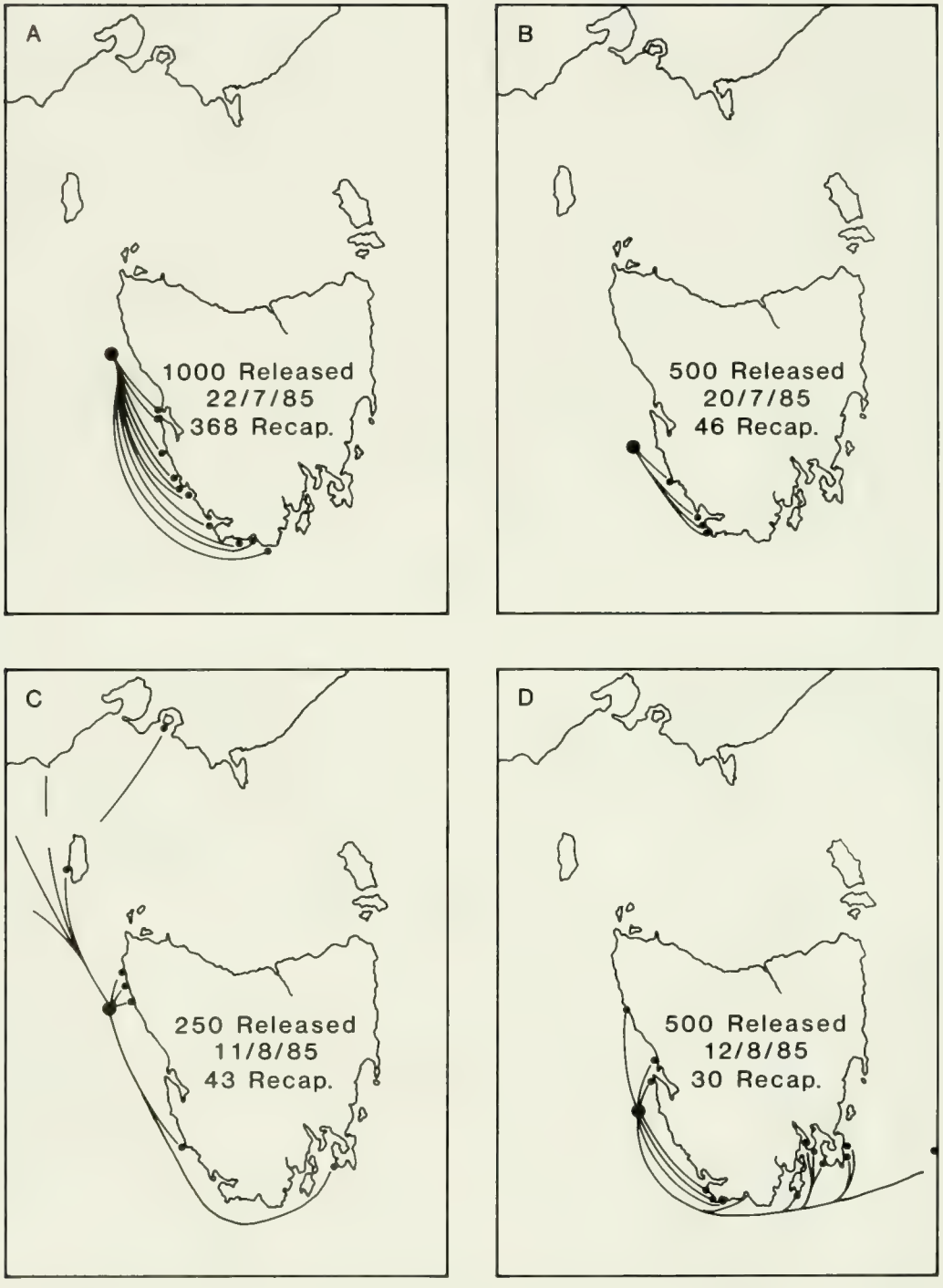

FIGURE 7.—Release and recovery points of surface drift cards for the first (20 and 22 July 1985, A and B) and second (11 and 12 August 1985, C and D).

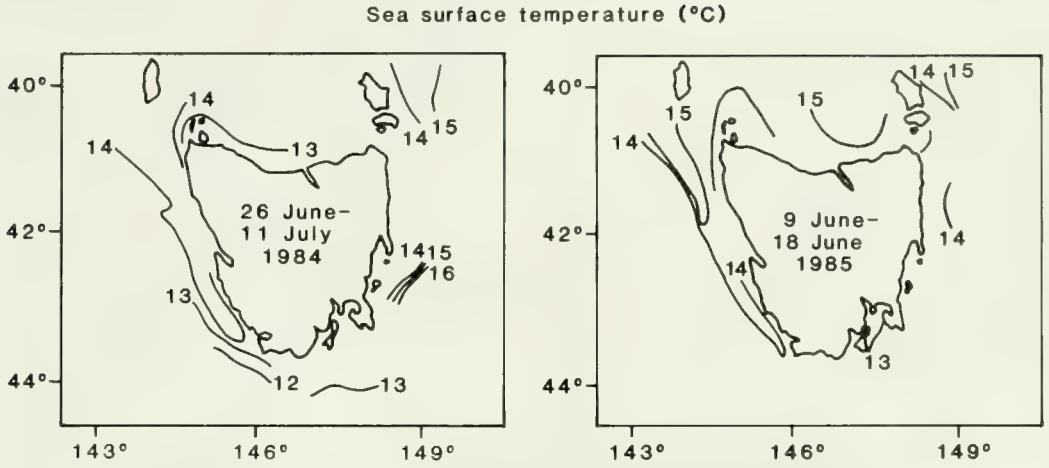

FIGURE 8.—Distribution of surface isotherms during early winter of 1984 and 1985, based on shipboard thermosalinograph traces.

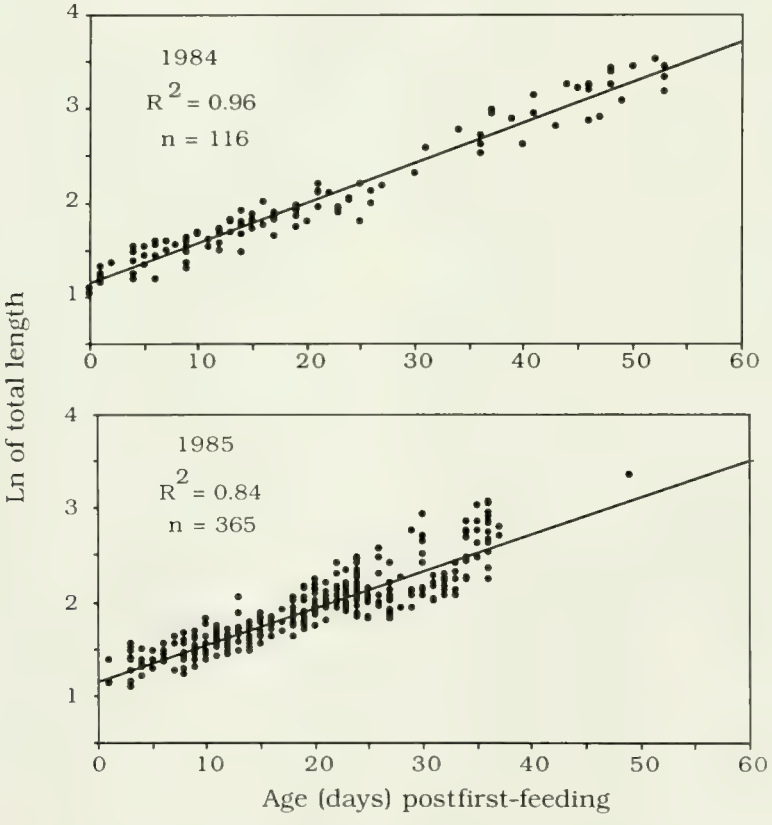

FIGURE 9.—Regressions of ln total length against age (days postfirst feeding) for 116 larvae of *Macruronus novaezelandiae* collected in 1984 and 365 larvae collected in 1985. A semilog regression accounts for 96% of the variance in length at age in 1984 and 84% of the variance in 1985. Differences between years in the slopes of the regressions are significant at $P < 0.01$.

Individual variability in rates of larval growth was assessed by examining the distribution of residuals around the mean exponential growth trajectory for each population each year; a positive residual indicates growth faster than average for the population and a negative one growth slower than average. Analysis of these residuals indicated that rates of larval growth varied seasonally in both years (Fig. 10). Although the variability of rates of larval growth was high within any given period, in both years growth residuals differed significantly for larvae hatched in different months (ANOVA $F_{5,110} = 6.72$, $P < 0.001$, for 1984, and $F_{3,361} = 50.86$, $P < 0.001$, for 1985). In 1984, there was a weak, but consistent tendency for residuals to increase throughout the spawning season (correlation between residual and hatching date, $r = 0.36$, $P < 0.01$). In 1985, deviations from population mean growth rates were generally negative early in the spawning season, reached a positive maximum during August, and then declined in September.

There was also evidence of a complex relationship between rates of larval growth and location. Overall, the distributions of growth residuals differed significantly across transects ($F_{9,355} = 8.71$, $P < 0.01$), with relative growth rates tending to be highest farthest from the west coast spawning area. The weakness of the correlation between growth rate and distance is due, in part, to two factors. First, there was a marked change in the relationship between location and growth rate with increasing age of the larvae examined. The older the larvae, the more positive the slope between distance from the spawning area and relative growth rate (Fig. 11). For larvae less than approximately 10 d postfirst-feeding, the slope was significantly

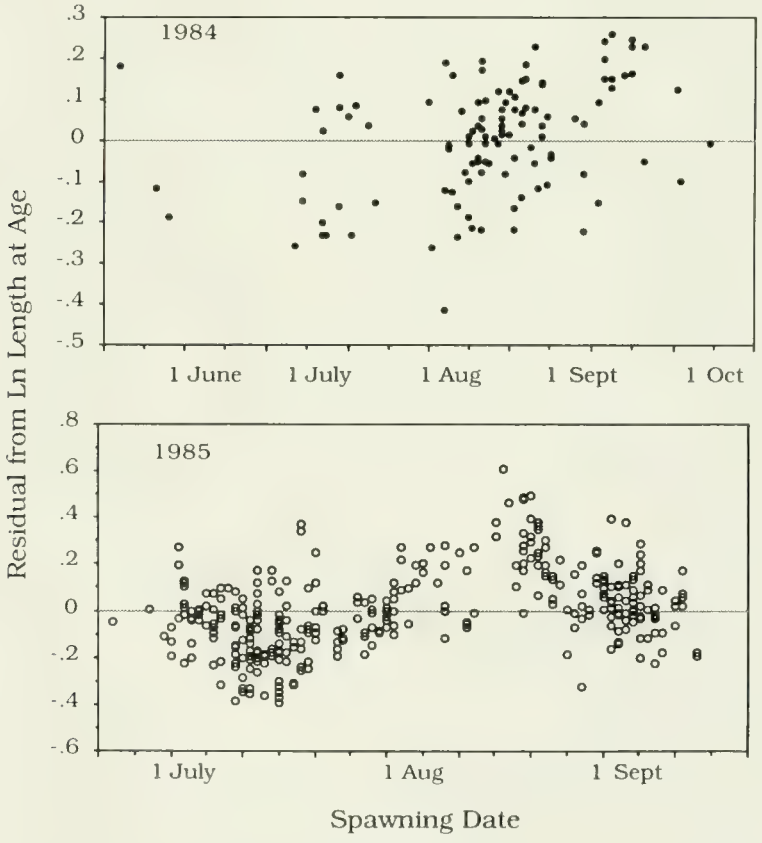

FIGURE 10.—Temporal variation of residuals from the semilog regression of ln total length against age for 1984 and 1985. *Macruronus novaezelandiae* spawning started approximately a month later in 1985 than 1984 (see Gunn et al. in press for details). Differences in residuals for larvae pooled by month of spawning are significant at $P < 0.01$ for both years.

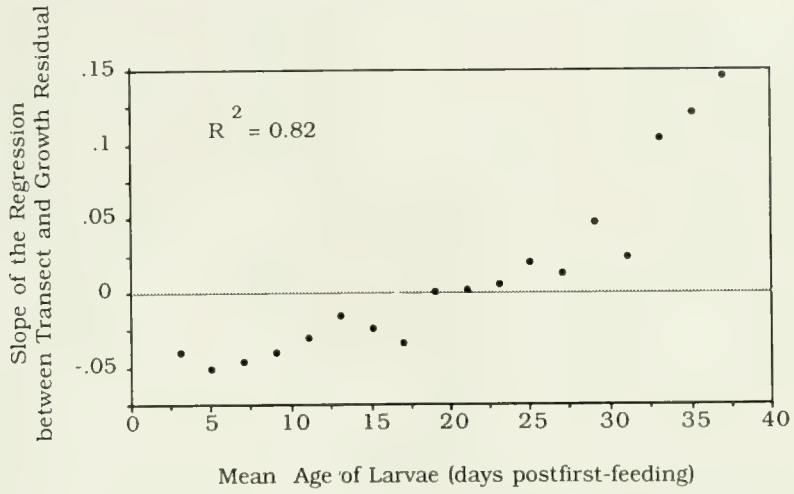

FIGURE 11.—Relationship between age of *Macruronus novaezelandiae* larvae examined (pooled into 3 d increments) and the slope of the regression between relative growth rate (residual from semilog regression of ln total length against age) and transect number. The correlation between slope of the regression line and age class of larvae is significant at $P < 0.01$.

negative; relative growth rates were highest on the west coast, near the spawning area, and declined to the south and east ($F_{1,106} = 20.25$, $P < 0.001$) (Fig. 12). In contrast, for larvae older than approximately 25 d postfirst-feeding, the slope was significantly positive; relative growth rates were lowest on the west coast, increased towards the east coast ($F_{1,124} = 25.58$, $P < 0.001$), and were highest farthest from the spawning area (Fig. 12). The transition from a negative (west coast fastest) to a positive (east coast fastest) slope occurs at a larval age of approximately 17–22 d postfirst-feeding.

The second factor confounding the correlation between distance from the spawning ground and relative growth rates is an apparent seasonal change in the strength of the correlation, particularly for older larvae. A correlation between distance from the west coast and relative growth rates of larvae accounts for 27% of the variance in growth residuals for larvae aged more than 25 d postfirst-feeding in the early, slow-growth portion of the 1985 spawning season. By August, however, during the period when larval growth rates were uniformly high, the correlation accounts for only 10% of the variance in growth rates and, by the end of the spawning season, for larvae hatched after 25 August, the relationship between location and growth rates for these older larvae disappears altogether ($R^2 = 0.02$). There are insufficient data for a comparable analysis of seasonal changes in growth rates of older larvae in 1984.

DISCUSSION

The increase in mean age and size of larvae with increasing distance from the west coast, the pattern of drift card returns, and the distribution of surface isotherms on the west coast of Tasmania during winter all support the hypothesis that larval *M. novaezelandiae* are transported by longshore currents from a spawning ground on the west coast to the southeastern and eastern coasts. This hypothesis is also supported by independent studies of the physical oceanography of the west coast. A southward flowing, longshore current off the west coast in winter was first suggested by Newell (1961); drift bottles he deployed off the coast moved in a similar pattern to our drift cards. Subsequently, Baines et al. (1983) inferred the presence of this current from a shelfward depression of isotherms and confirmed it by the drift pattern of a drogue released off the northwestern coast. Baines et al. (1983) reported the Zeehan Current, as they named it, to be relatively narrow (approximately 40 km wide) and restricted largely to the edge of the continental shelf. It moves southwards at a depth averaged flow in the order of about 20 km/d (C. Fandry, pers. commun.[6]). This figure is reasonably consistent with our data on larval ages at different points along the advection route. The distance between the spawning ground

[6]C. Fandry, CSIRO Division of Oceanography, GPO Box 1538, Hobart, Tasmania 7001, Australia, pers. commun. June 1987.

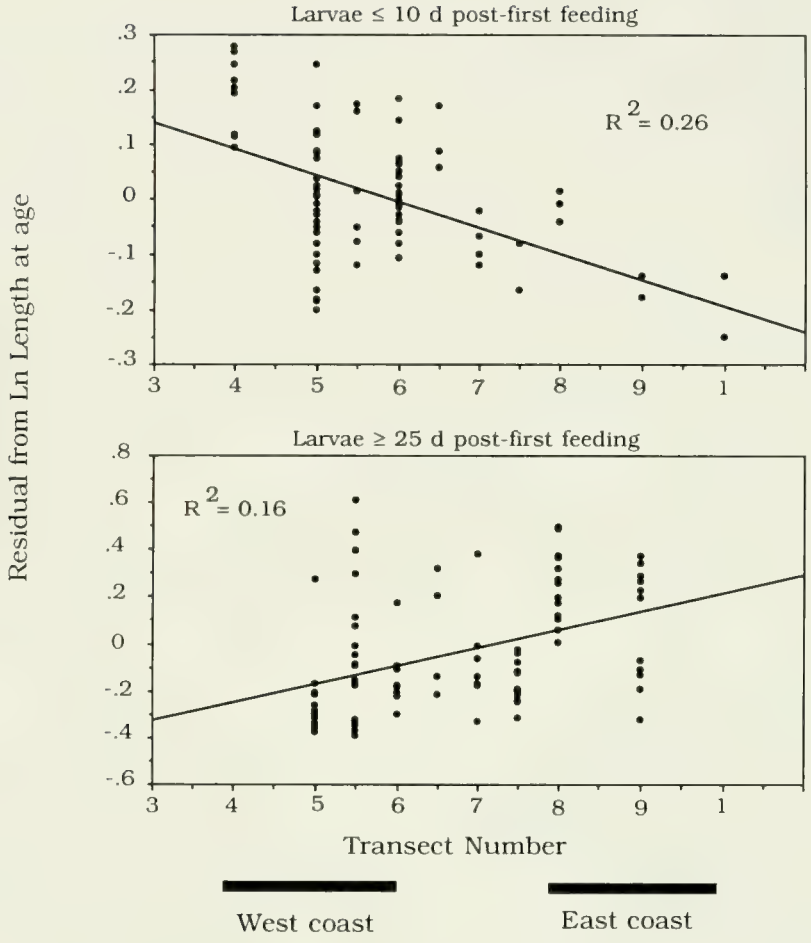

FIGURE 12.—Regressions between relative growth rates and transect number for *Macruronus novaezelandiae* larvae ≤10 d postfirst-feeding and those ≥25 d postfirst-feeding. Correlations are significant at $P < 0.01$ for both age classes of larvae.

and transect 8, off the southeastern coast, for example, is about 400 km. Hence, the minimum time it should take a larva drifting passively in the mainstream of the current to reach transect 8 would be approximately 20 days. In fact, the shortest interval between release time and recovery of one of our drift cards on the southeastern coast was only 15 days suggesting that at least occasionally larvae could be transported around the southern end of Tasmania very quickly. Total ages of larvae collected at transect 8 varied from 22 to 41 days, averaging 31 days in 1984 and 32 days in 1985. As few larvae are likely to traverse a perfectly direct path between the spawning grounds and transect 8, the mismatch between predicted minimum and observed average ages is probably reasonable and the hypothesis that larval distributions are the result of passive advection seems plausible.

The range of ages of larvae at each point along the advection route appears to reflect, in part, spawnings by *M. novaezelandiae* at sites north and south of the primary spawning area, in part, the distribution of the larvae relative to the main axis of the Zeehan Current, the location of which is likely to vary with time, and, in part, variations in the strength and direction of that current. Baines et al. (1983) noted that the manifestation of the current may often be overridden by direct wind effects, which is supported by our observations. The drift rate and direction of our drogue varied as an immediate function of wind speed and direction. C. Fandry (fn. 6) suggested that wind affects move-

ment of the water column off the west coast to depths of at least 100 m, i.e., virtually the entire depth range occupied by larval *M. novaezelandiae*. Hence, it is likely that the direction and speed of larval transport vary, though still being predominantly southwards. Such variability is indicated by our drift card data. Drift cards released at the mid-shelf station of transect 5 on 22 July 1985 were recovered inshore and south of the release point; cards released at the same location 19 days later, however, were mostly recovered north of the release point (Fig. 7). Given the depth of the wind-driven effects, it is likely that larval fishes present at that site on the two dates would also have been advected either south or north, depending on temporary conditions of wind and current.

Indeed, some larvae apparently develop wholly off the west coast. In both years of the study, the range in sizes and ages of larvae at transect 5, just north of the spawning grounds, was nearly as wide as those at all other transects combined. On this basis, we suspect that some oceanographic feature on the mid-west coast of Tasmania results in significant retention of larvae in that area. One possibility is that, as larvae are most abundant near shore, some are trapped in relatively static pockets of water near the coast and not entrained in the general southerly current stream. Another possible retention mechanism is a coastal gyre, as yet unreported, that perhaps forms in the winter off the west coast. Indeed, our sea-surface temperature data consistently show a westward bend of surface isotherms immediately offshore of transect 5, which could indicate such a gyre.

Whatever the retention mechanism, a consequence is that larvae vary widely in the location at which they undergo planktonic development. Such variability is not trivial in *M. novaezelandiae*. Apparent rates of larval growth in the species vary significantly both with time and location: faster in 1984 than in 1985, faster in some months than in others, and faster off the west coast for young larvae and off the east coast for older larvae. There are two ways these differences can be interpreted: either the differences are real and reflect variability in conditions that promote growth of larvae, or they are only apparent, deriving not from variations in growth rates, but from growth-dependent mortality that varies in intensity in time and space.

Testing these hypotheses directly in the field is difficult. They can be tested indirectly, however, by examining the distributions of residuals around the population-mean growth trajectories. Consider three possibilities: first, local differences in growth are real and are determined wholly by food availability; second, local variation is real, but upper and lower limits to growth are determined by physiological constraints inherent in the metabolism of the larvae; and third, real growth rates do not vary locally, but appear to differ due to variably intense selection (predation) against slower growing larvae. The first hypothesis (unconstrained growth) implies normal distributions of growth rates around population means for both fast and slow growing populations; the variance may alter with the mean, but skewness should not. The second hypothesis (constrained growth), however, implies distributions of growth residuals will vary with mean growth rate: the distribution will be negatively skewed (to the left) when mean growth rate is high (more individuals near the maximum growth rate) and positively skewed (to the right) when mean growth rate is low (more individuals near the minimum growth rate). The third hypothesis (growth-dependent mortality) also implies a relationship between the distribution of growth residuals and apparent mean rates of growth, but the relationship is opposite that implied by the constrained growth hypothesis. If predators selectively remove slow growing larvae, such mortality will skew distributions of growth residuals to the right. The greater the intensity of growth-dependent predation (= the higher the apparent mean growth rate), the more positive the skew. Hence, the growth-dependent mortality hypothesis implies that when apparent mean growth rate is low, the distribution of residuals should be normal or only weakly positively skewed; when apparent mean growth rate is high, the distribution should be skewed strongly to the right.

These predictions can be applied to field data for *M. novaezelandiae*. The mean growth rate of larvae was higher in 1984 than in 1985 and, for older larvae, was higher on the south and east coast than on the west coast (too few young larvae were caught on the east coast to warrant a comparison for that age group). The distributions of residuals for 1984 and 1985 are depicted in Figure 13, and those for west and southeast coast populations of larvae older than 25 d postfirst-feeding are depicted in Figure 14. The data are throughout consistent with the constrained-growth-rate hypothesis. As predicted by this hypothesis, the distribution of growth residuals is skewed negatively, albeit weakly, in 1984 ($k_2 = -0.35$, $t = 1.58$, $P < 0.1$), and skewed positively, also weakly, in 1985 ($k_2 = 0.45$, $t = 1.36$, $P < 0.1$). Similarly, growth residuals for the relatively fast-growing larvae caught off the south and east coasts are distributed normally ($k_2 = 0.25$, $t = 0.61$, NS),

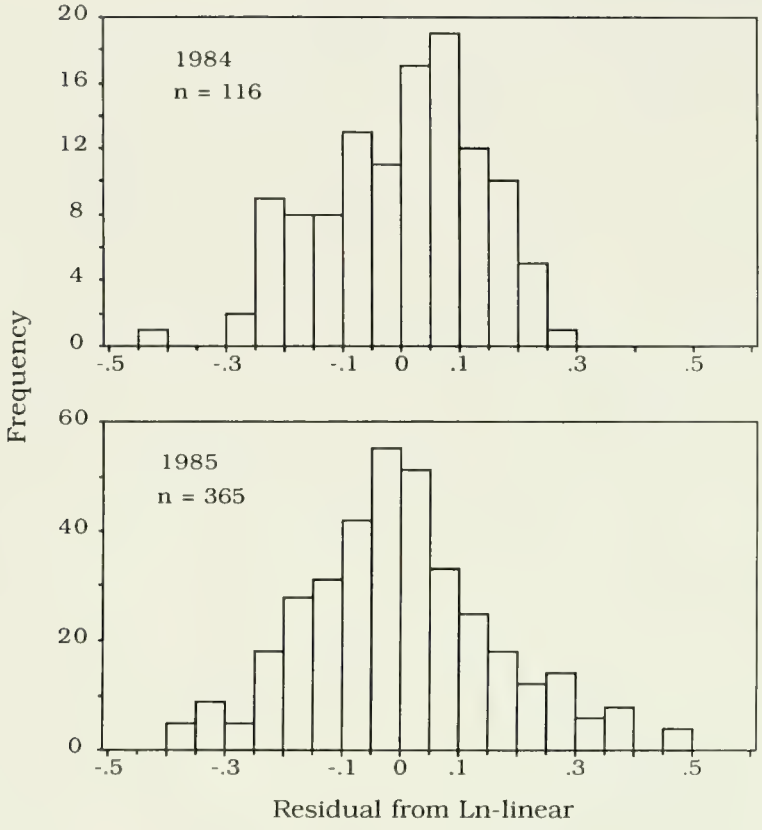

FIGURE 13.—The distribution of residuals about the semilog regression of ln total length against age of *Macruronus novaezelandiae* for 1984 and 1985, based on growth trajectories pooled by year.

whereas those for the slower growing larvae collected off the west coast exhibit a significant positive skew ($k_2 = 0.68$, $t = 2.76$, $P < 0.01$). We conclude, therefore, that the data are consistent with the constrained growth hypothesis, that variations in rates of larval growth documented in this study are likely to be real, operating within whatever factors constrain the limits of larval growth for the species, and that they reflect variations in environmental conditions that affect growth rates.

Exactly what these environmental conditions are is still not clear, though it is likely they relate to water temperature and food availability. That larvae <15–20 d postfirst-feeding grew faster off the west coast of Tasmania than off the south and east coasts could, for example, reflect the presence of the relatively warm Zeehan Current off the west coast. Growth rates of gadoid larvae increase with water temperature (Lawrence 1978) and temperatures in this current near the spawning grounds were 1°–2°C warmer than off the south and southeastern coasts. Circumstantial evidence suggests that regional differences in growth rates of older larvae, in turn, were related to differences in food availability. As noted above, larvae older than 25 d postfirst-feeding grew faster off the east coast than off the west coast early in the spawning seasons. This difference between coasts narrowed later in the season and disappeared altogether late in the spawning season (September). This pattern of spatial and temporal differences in growth was matched by variations in coastal productivity. Harris et al. (1987) reported that in winter (August, referred to by them as "early spring"), autotrophic water column productivity was higher off the east coast in 1985 than off the west coast; reported values for shelf waters ranged from 1.71 to 4.5 mg $C \cdot m^{-3} \cdot h^{-1}$ for the east coast versus 0.06 to 0.84 for the west coast. In September, however, (Harris et al.'s "late spring"), differences in water column

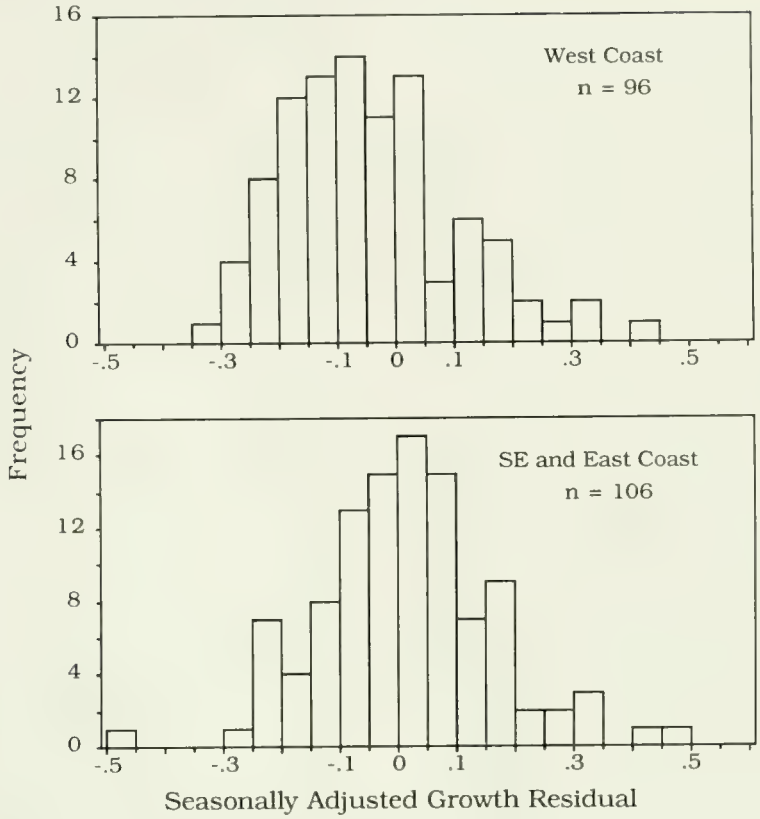

FIGURE 14.—The distribution of seasonally adjusted residuals from the semilog regression of ln total length against age for *Macruronus novaezelandiae* larvae ≥25 d postfirst-feeding for larvae collected off the west coast (transects 5 and 6) and the southeast and east coasts (transects 8 and 9). Residuals were adjusted for seasonal variations in mean rates of larval growth by fitting a polynomial to the seasonal patterns and extracting new, detrended residuals.

productivity between the two coasts were less pronounced; measured values for two sites off the east coast were 1.51 and 2.89 mg $C \cdot m^{-3} \cdot h^{-1}$ versus values for the west coast that ranged from 1.04 to 2.24. We suspect, therefore, that growth rates of these older larvae are driven by local differences in the abundance of copepods and other larger zooplankters that constitute their primary diet. Why such regional differences in productivity did not result in a parallel difference between coasts in growth rates of younger larvae is not known. It may be that the effects of food availability on growth rates of first-feeding larvae are overridden by those of water temperatures.

Regardless of how location affected the growth rates of young and older larvae, summarized in Figure 11, the net effect remains that conditions favorable for early larval growth were not spatially coincident with those favoring growth by older larvae. Specifically, growth rates of larvae aged <10–15 d postfirst-feeding were highest closest to the spawning area of *M. novaezelandiae*, whereas growth rates of larvae older than 25 d postfirst-feeding increased the farther away from the spawning area the larvae were caught. Why *M. novaezelandiae* aggregate to spawn off the west coast of Tasmania in the winter, rather than at any other site or time, cannot be known. Winter spawnings are not the norm in gadoids (Breder and Rosen 1966; Hislop 1984) nor, with the possible exception of a weak gyre off the coast, is there any conspicuous oceanographic feature or condition, such as a highly localized plankton bloom, yet documented that would uniquely characterize the site as a particularly good one for spawning. Nonetheless, the enhanced growth rates of early stage larvae at the site argue

for a positive selective value for migrating to the west coast to spawn. At the same time, increased rates of growth by older larvae away from the spawning area suggest equally strong selection to ensure that, as they develop, larvae are transported away from the west coast. Larvae achieve the maximum growth rate only by being at the right place at the right stage of their development. Hence, migration of *M. novaezelandiae* to a specific spawning area and subsequent contra-natant migration of larvae away from that spawning area appears to be neither evolutionarily trivial nor solely the result of selection to place eggs and larvae upstream of some specific nursery habitat. Rather, it is an adaptive feature of the reproductive biology of the fish that relates directly to elements of its larval ecology.

Further, if survival of larvae varies with growth rate, as has been widely suggested (Hunter 1981; Rosenberg and Haugen 1982; Folkvord and Hunter 1986), then spatial effects on rates of larval growth can provide a mechanism that links current variability with year-class strength in *M. novaezelandiae*. We have, as yet, no direct evidence for such a link in this species but such a hypothesis has been frequently proposed for marine fishes (Walford 1938; Sette 1943; Harden Jones 1968; Nelson et al. 1977; Parrish et al. 1981). In most cases, however, emphasis has been placed on the adverse effects of advection, in which inappropriate current patterns result in larvae being transported into oceanic habitats not well suited for their development. For example, Devonald (1983) and Theilacker (1986) presented evidence that larval mackerel, *Trachurus symmetricus*, found well off the California coast feed less well and are in worse condition than those collected closer to shore, which is consistent with the adverse effects of offshore transport on year-class strength suggested by Parrish et al. (1981). In contrast, advection is not a negative factor in *M. novaezelandiae*: larvae do better when advected away from the spawning area at the right stage of their development. Such a positive effect of advection is implicit in hypotheses involving spawning grounds, nursery areas, and adult habitats that are spatially separated (Harden Jones 1968; Shelton and Hutchings 1982). Data for most species, however, are still too sparse to determine the general significance of a direct, positive effect of advection on rates of larval growth like that in *M. novaezelandiae*.

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AGE AND GROWTH OF KING MACKEREL, *SCOMBEROMORUS CAVALLA*, FROM THE ATLANTIC COAST OF THE UNITED STATES[1]

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ABSTRACT

Whole sagittae from 683 and sectioned sagittae from 773 "adult" (age > 0 ; 437–1,310 mm FL), and lapilli from 29 larval (2–7 mm SL) and 69 young-of-the-year (79–320 mm FL) king mackerel, were examined. All fish were from waters off the Atlantic coast of the southeastern United States (Cape Canaveral, Florida to Cape Fear, North Carolina). Back-calculated lengths at ages and von Bertalanffy growth equations were calculated from both whole and sectioned sagittae. Ages determined from sectioned sagittae were significantly greater than ages determined from whole sagittae, and the magnitude of the difference increased with age (from sections). Rings on sectioned sagittae are considered to be true annual increments, forming during June–September. There was no clear pattern to ring formation on whole otoliths. The oldest fish examined was age 21. The daily nature of rings on lapilli of age 0 king mackerel was not validated, but if the marks are formed daily they suggest growth rates of approximately 0.47 mm/d for early larvae and 2.9 mm/d for fish 1–3 months of age.

The king mackerel, *Scomberomorus cavalla*, is a migratory pelagic scombrid occurring in coastal waters of the western Atlantic from Massachusetts to Brazil and throughout the Gulf of Mexico (Collette and Russo 1984). In the United States, this fish is highly sought by both commercial and recreational fishermen from North Carolina to Texas (Manooch 1979; Trent et al. 1983). Decreased abundance in part of its range has lead to the establishment of landings quotas and limits.[3] Tagging studies indicate that king mackerel from the Atlantic coast and those from the Gulf of Mexico form separate migratory groups, with some overlap and mixing in the waters of southern Florida.[4] Biological studies in each geographic area are essential due to the importance of the species, possible reproductive isolation of the groups, and the potential for group-specific life history traits. Considerable research effort has been directed toward king mackerel in the Gulf of Mexico, but fish from the Atlantic coast of the United States, especially north of Florida, have received little attention. Beaumariage (1973) utilized fish from both coasts of Florida, but the only sample he had from northeastern Florida was combined with the rest of his data. Similarly, Johnson et al. (1983) sampled fish from North Carolina and South Carolina, but they were pooled with larger samples from the Gulf of Mexico. A more recent study (Manooch et al. 1987) utilized only Gulf of Mexico fish. Thus, there are no previous studies of Atlantic group king mackerel on which to base management.

Despite evidence that otolith sections may give more accurate ages than whole otoliths in long-lived species (Beamish 1979), major studies of king mackerel age and growth have been based principally on data derived from whole otoliths (Beaumariage 1973; Johnson et al. 1983; Manooch et al. 1987). Adequate validation of the use of whole sagittae has apparently been achieved in at least one of these investigations (Manooch et al. 1987), but we encountered difficulties in the interpretation of whole otoliths while using similar methods in the present study. This report describes age and growth of king mackerel from the Atlantic coast of the southeast United States, compares results from whole and sectioned otoliths, and describes presumed daily growth of larval and young-of-the-year (YOY) king mackerel from the same geographic area.

METHODS

King mackerel were collected along the Atlantic coast of the southeastern United States (lat 29° to

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[3]South Atlantic Fishery Management Council, Charleston, SC. News release, 7 July 1987.

[4]Powers, J. E., and P. Eldridge. 1983. Assessment of Gulf of Mexico and south Atlantic king mackerel. Unpubl. manuscr., 24 p. Southeast Fisheries Center, National Marine Fisheries Service, NOAA, Miami, FL 33149.

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Fishery Bulletin, U.S. 87:49–61.

35°N) from May 1983 through January 1987. "Adult" (= age >0) fish were caught on hook and line in the recreational fishery, in the commercial fishery, and during research cruises aboard the RV *Oregon* and RV *Lady Lisa*. Most YOY kings were collected during research cruises aboard the RV *Lady Lisa* and RV *Carolina Pride* using trawls of various types, but some fish were taken with gill nets, seines, and from commercial shrimp trawling bycatch. Larvae were collected from the RV *Oregon* with bongo (505 μm mesh) and neuston (505 or 947 μm mesh) nets, and were preserved in 95% ethanol.

Nonlarval king mackerel were weighed and measured (total length [TL] and fork length [FL]), while larvae were measured to the nearest mm standard length (SL) using a dissecting microscope and ocular micrometer. Sagittae of adults were removed and stored dry, and gutted fish and gonads were weighed when possible. All otoliths were removed from larval and YOY fish. Larval otoliths were mounted on microscope slides, while otoliths from YOY fish were stored in 75% ethanol.

The lapillus was the best structure from which to count presumed daily rings for both larval and YOY king mackerel.[5] Larval lapilli were immersed in oil on a microscope slide and viewed with transmitted light at 623× on a microscope equipped with a video camera. Two readers made three counts for each of 29 larvae (2–7 mm SL), and the mean of the six counts, rounded to the nearest integer, was used to estimate the number of presumed daily rings. Lapilli from 69 YOY fish (79–320 mm FL) were prepared by a series of polishings on a smooth whetstone, on 600 grit sandpaper, and on glass with a fine liquid abrasive (AO Scientific Instruments Cat. No. 938C[6]). Polishing continued until rings in the central portion of the lapillus became visible, and readings were made in the same manner as those for larvae. Some lapilli were also read from photomicrographs taken with a scanning electron microscope (SEM) to determine differences in marginal increments (distance from the distal edge of the outer ring to the otolith margin) between fish caught at different times of day.

Whole sagittae from 683 adult fish were examined. Otoliths were placed in a dish of cedarwood oil and viewed, concave side up, under a dissecting microscope (12×) with reflected light. Measurements from the focus to the distal edge of each opaque ring, and from the distal edge of the last opaque ring to the otolith margin, were made with an ocular micrometer along an axis approximating the extension of the sulcus acousticus (Johnson et al. 1983). The marginal increment was zero when an opaque ring occurred at the otolith margin. Transverse sections (ca. 0.5 mm thick) of one sagitta from each of 773 fish, including otoliths also read whole, were made through the focus on a plane perpendicular to the long axis with a Buehler Isomet low speed saw. Sections were viewed at 50× in the same manner as whole sagittae. The focus was not always definite on sections, so measurements were standardized by defining the focus as the midpoint of a line connecting the two most distant points of the first ring. This convention closely agreed with actual focus locations for sections in which the focus was apparent. Because the axis of sagittal growth changed after the first year, sections were measured in two parts: 1) from the focus to that point on the first ring, on the dorsal side of the sulcus acousticus, which minimized the length of the line without crossing the sulcus acousticus, and 2) from the first ring to the margin of the section, on a line perpendicular to the rings, along the recognizable major axis of sagittal growth after year 1. Additional sections were made of sagittae from 10 randomly chosen fish: one longitudinal section, and two sections at 45° perpendicular to each other. The purposes of these sections were to determine if there was evidence for splitting of rings and to ensure that the transverse section, described above, was the most legible preparation. All whole and sectioned sagittae were examined by two readers, and the age was excluded from analyses if the readers did not agree. Sex was determined by gross examination and was verified histologically in subsamples. Regressions of fork length on otolith radius were performed for sexes separately and combined. Back-calculated sizes at age were computed for males, females, and sexes combined by the Fraser-Lee method (Carlander 1982; Poole 1961). The SAS NLIN procedure (SAS Institute 1982) was used to fit von Bertalanffy equations to the weighted mean back-calculated lengths at age.

RESULTS

The astericus was not detected in any larvae, suggesting it forms at >7 mm SL. All larval lapilli had well-defined presumed daily rings that were easily

[5]Waltz, C. W. 1986. Evaluation of a technique for estimating age of young-of-the-year king (*Scomberomorus cavalla*) and Spanish (*S. maculatus*) mackerels. Unpubl. manuscr. South Carolina Wildlife and Marine Resources Department, Marine Resources Research Institute, P.O. Box 12559, Charleston, SC 29412.

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

counted with good agreement between readers. The regression of mean ring count (R) on SL is $R = 0.11 + 1.56$ (SL); $n = 29$; $r^2 = 0.73$ (siginificant at $P < 0.001$). That r^2 is not higher is attributed to coarse length measurements (nearest mm). If the rings are daily, the regression of SL on R (SL = 1.15 + 0.47(R)) indicates a growth rate of 0.47 mm SL/d for early larvae (Fig. 1).

Presumed daily ring counts were obtained for 54 (78%) of 69 YOY king mackerel 79–320 mm FL. A strong correlation was found for the regression of mean ring count (R) on FL ($R = 2.0 + 0.32$(FL); $n = 54$; $r^2 = 0.92$, significant at $P < 0.001$). If these rings are actually daily, the regression of FL on R (FL = 7.25 + 2.91(R)) suggests that a growth rate of 2.9 mm/d occurs at 30–100 days of age (Fig. 2). Attempts to produce evidence for the daily nature of these rings by measuring diel variation in marginal increments using SEM were not successful, perhaps due to inadequate specimen preparation. Rings were normally visible on portions of the lapilli, but we could not consistently read increments near the margin.

Two readers agreed on annual ring counts for 77% of all whole sagittae and 70% for fish >850 mm FL, resulting in 15 age (= number of rings) classes. Examination of sections made in the four planes verified that sections perpendicular to the long axis of the sagitta were most legible, and no evidence for splitting of rings was found. Agreement on reading sections was greater than that for whole sagittae, with counts verified on 90% of all sections and 96% from fish >850 mm FL. The oldest fish aged from sections was age 21. Agreement between the two techniques was but 47% among fish on which both whole sagittae and sections were used, and the ages were significantly different (t test for paired observations: $P < 0.001$). Counts were very similar for the first three to five age classes, but sections from older fish commonly showed one or more rings not detected on whole sagittae and the difference increased with age. The two procedures differ at an earlier age for males than for females (Fig. 3).

The correlations of fish length with otolith radius were significant ($P < 0.001$ for all) for whole and sectioned sagittae of males, females, and sexes combined (Table 1). Plots of focus-ring measurements from sections for successive age groups through age 5 show that the distribution was unimodal for each increment, that distances to the rings varied little with age, and that overlap increased with age (Fig. 4). The pattern for whole sagittae was not quite as well defined (Fig. 5). Back-calculated lengths at ages from whole and sectioned otoliths agree well with observed lengths, especially among (younger) age groups with large sample sizes (Tables 2–7). Annual growth increments from whole and sectioned otoliths were generally higher for females than males, especially during the first few years of life. Lengths at age determined from whole otoliths were con-

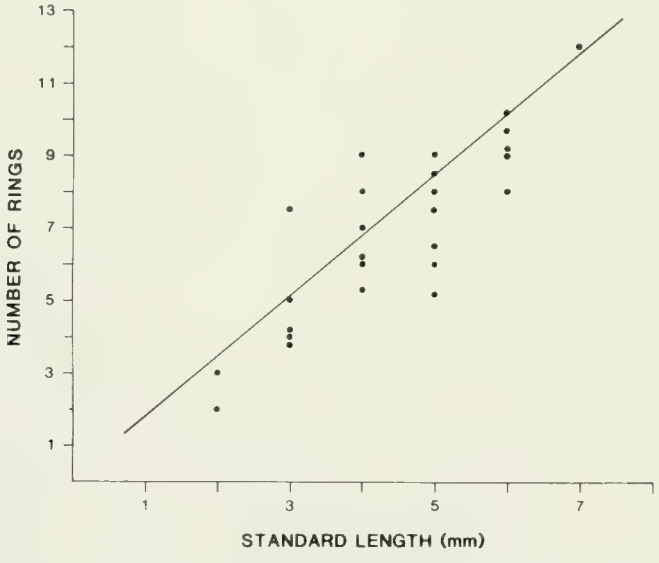

FIGURE 1.—Regression of number of presumed daily rings on standard length of larval king mackerel.

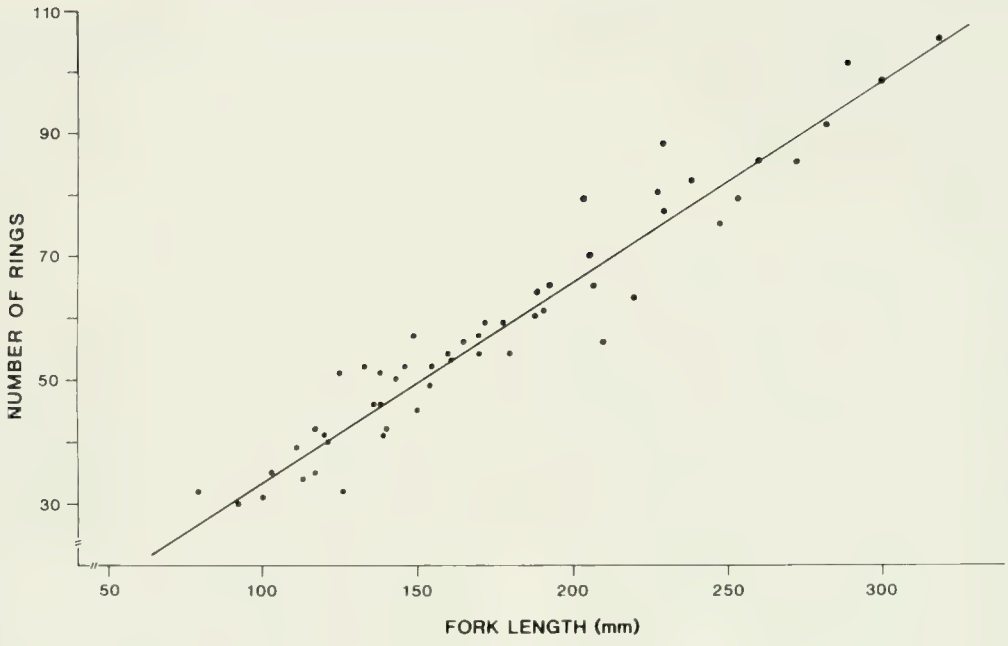

FIGURE 2.—Regression of number of presumed daily rings on fork length of young-of-the-year king mackerel.

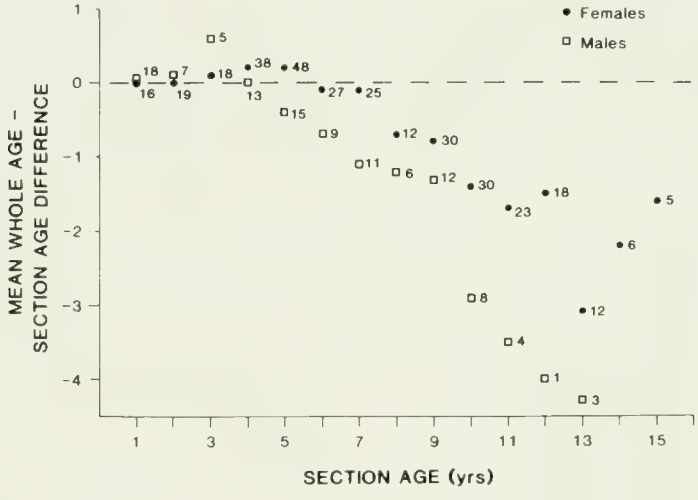

FIGURE 3.—Mean difference between whole and sectioned otolith ages for each sectioned age group, by sex. Sample size is indicated for each data point.

TABLE 1.—Least squares regression of fork length (FL, in mm) on otolith radius (OR, in ocular units) for sectioned and whole otoliths.

	Sectioned			Whole		
		N	r^2		n	r^2
male	$\log_{10}$ FL = 1.088 + 1.012 $\log_{10}$ OR	204	0.90	$\log_{10}$ FL = 1.242 + 0.918 $\log_{10}$ OR	172	0.80
female	$\log_{10}$ FL = 1.209 + 0.967 $\log_{10}$ OR	448	0.83	$\log_{10}$ FL = 1.116 + 1.002 $\log_{10}$ OR	409	0.77
combined	$\log_{10}$ FL = 1.350 + 0.884 $\log_{10}$ OR	704	0.80	$\log_{10}$ FL = 0.773 + 1.184 $\log_{10}$ OR	632	0.83

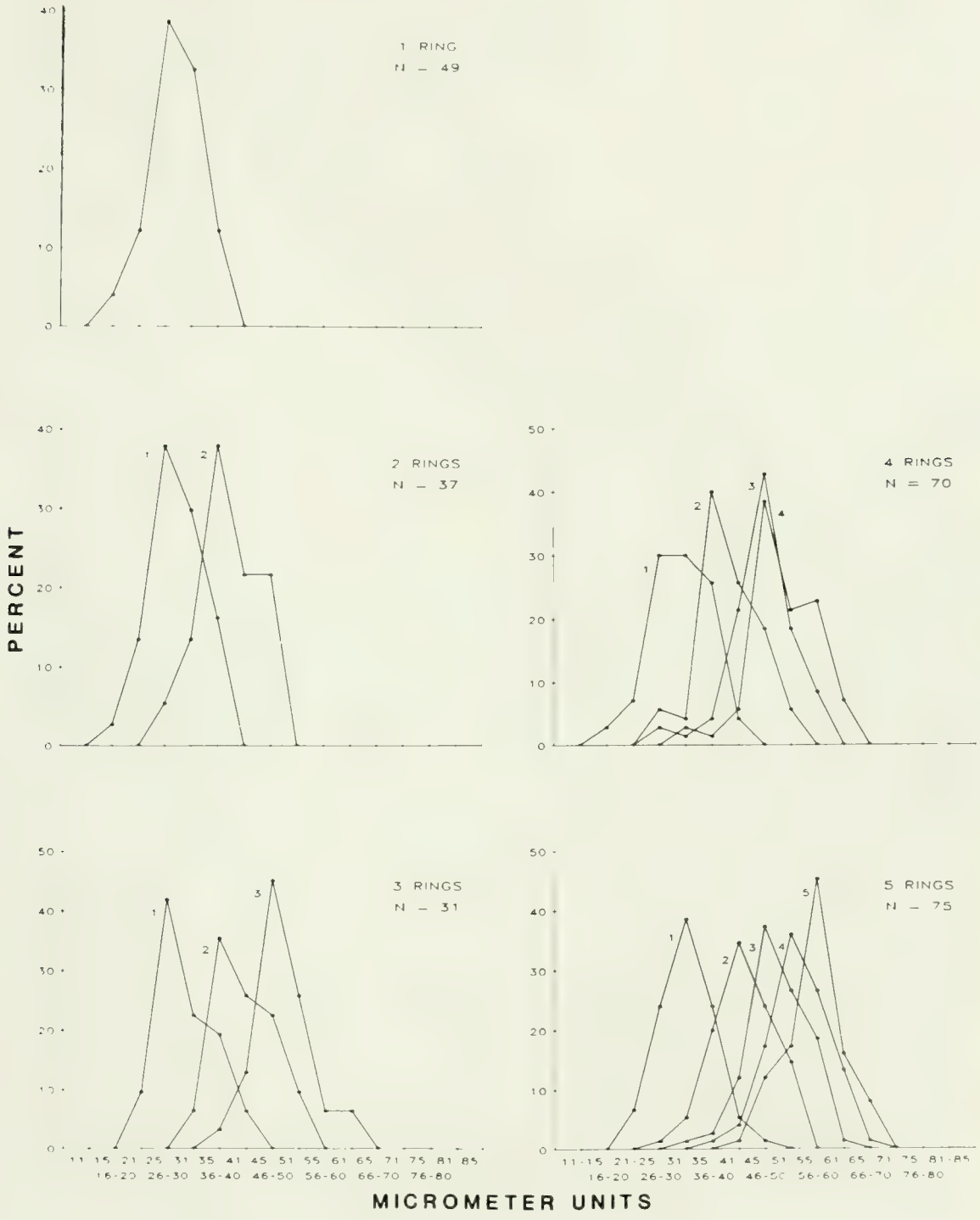

FIGURE 4.—Distributions of focus-ring distances from otolith sections for age groups one through five.

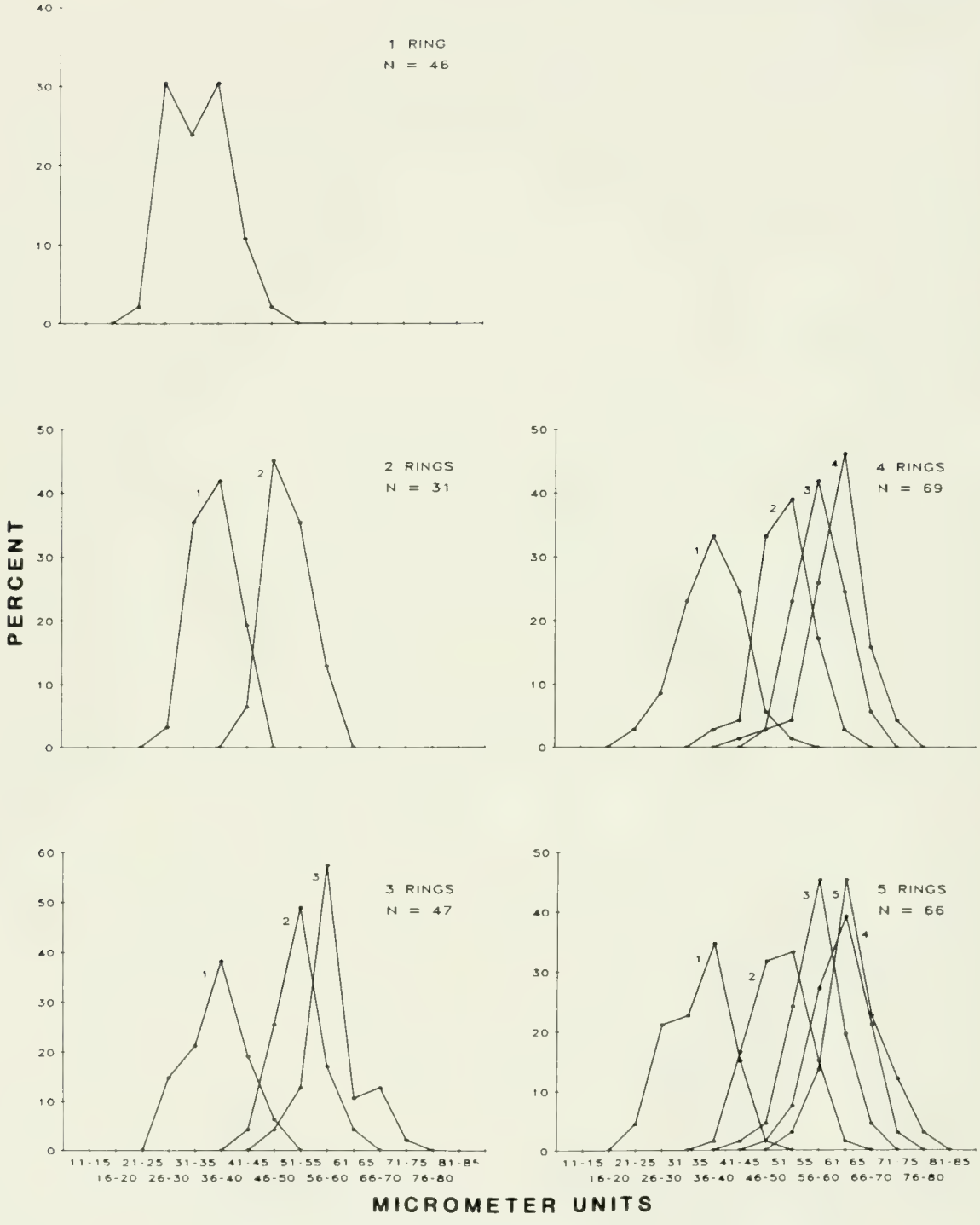

FIGURE 5.—Distributions of focus-ring distances from whole otoliths for age groups one through five.

TABLE 2.—Mean fork lengths (mm) at capture and mean back-calculated fork lengths at ages from sectioned otoliths of male king mackerel.

Age	No. of specimens	Mean length at capture	Mean back-calculated lengths at successive annuli															
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	19	511	433															
2	7	716	479	649														
3	6	758	457	615	712													
4	16	791	465	601	690	754												
5	17	808	440	585	670	730	778											
6	14	825	441	580	652	712	759	805										
7	19	838	417	566	647	698	743	784	819									
8	11	884	455	600	666	716	757	792	826	862								
9	16	882	434	569	643	692	734	769	803	833	864							
10	13	882	404	546	612	670	709	744	773	805	836	867						
11	8	912	419	545	614	663	702	742	774	806	833	865	895					
12	10	909	387	532	597	641	681	718	748	780	810	838	863	892				
13	11	918	366	516	585	635	673	706	739	768	798	826	851	878	907			
14	7	954	375	505	581	630	673	706	742	773	805	833	857	884	911	938		
15	5	930	383	507	581	623	657	687	718	743	770	797	822	844	871	894	919	
16	3	948	383	475	547	607	646	677	709	737	758	787	815	839	864	892	912	937
	Total number		182	163	156	150	134	117	103	84	73	57	44	36	26	15	8	3
	Weighted mean		426	566	639	689	724	753	779	801	822	839	857	875	896	914	916	937
	Growth increment		426	140	72	50	34	29	25	22	20	17	17	18	21	17	2	20

sistently greater than from sections, except for age 1 females (Fig. 6). The von Bertalanffy growth constants (K) from whole and sectioned otoliths are greater for males (Table 8), while females attain greater maximum length. Estimates of asymptotic length (L_∞) from both otolith preparations are conservative for both sexes.

The distribution of monthly percentages of sectioned otoliths with zero marginal increment was unimodal and reasonably normal, indicating annual ring formation that peaks in August–September (Fig. 7). Few section margins were opaque during October–May, though sample sizes were smaller then. Similar treatment of marginal increment data from whole sagittae produced completely different results: opaque margins seem to occur irregularly from March through November. This suggests either that readings of whole otoliths were often in error despite agreement between observers, or that rings were not true annuli.

DISCUSSION

The daily nature of rings on lapilli of larval and YOY king mackerel was not validated, although correlations between otolith radius and fish length were very strong. If the marks are daily, they imply a moderately high average growth rate for early larvae followed by very rapid growth (2.9 mm/d) for fish 1–3 months of age. Future studies should concentrate on validation, possibly by chemical (tetracycline, calcein) labeling of otoliths or by describing diel variations in marginal increments.

Readability (percentage legible enough for observers to agree on age) of sectioned otoliths was greater than that of whole otoliths, especially among fish >850 mm FL. The two techniques agreed only 47% of the time, primarily for smaller individuals. Why Johnson et al. (1983) and Manooch et al. (1987) found much higher agreement (96% and 87%, respectively) between whole and sectioned otoliths is not clear. The opacity and appearance of sagittae may differ between Gulf of Mexico and Atlantic king mackerel (pers. commun., S. P. Naughton[7]), and could account for differences in agreement. Beamish (1979) noted that readability and reliability of whole otoliths differed between stocks of Pacific hake, *Merluccius productus*, supporting this hypothesis. He reported a 47% agreement between whole and sectioned otolith ages and concluded that ages from sections were more reliable, especially in older age groups and for certain geographic areas. He also found even greater deviations that we found between ages from whole and sectioned otoliths, but utilized all readings. If our procedures were liberalized in a like fashion, or if readings from a single observer were used, we feel that the deviations reported here would be much greater.

[7]S. P. Naughton, Southeast Fisheries Center Panama City Laboratory, National Marine Fisheries Service, NOAA, Panama City, FL 32407, pers. commun.

TABLE 3.—Mean fork lengths (mm) at capture and mean back-calculated fork lengths at ages from sectioned otoliths of female king mackerel.

Age	No. of specimens	Mean length at capture	Mean back-calculated lengths at successive annuli																			
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	16	548	462																			
2	24	719	503	668																		
3	19	820	519	681	775																	
4	43	832	494	635	727	794																
5	51	878	500	650	739	804	856															
6	37	897	484	634	716	775	829	876														
7	30	937	487	632	718	778	831	876	919													
8	14	977	491	646	731	790	836	878	917	956												
9	39	990	477	616	709	768	815	857	896	937	975											
10	42	1,005	477	629	699	759	804	847	883	919	956	991										
11	32	1,052	482	630	710	765	812	855	893	929	964	998	1,034									
12	27	1,063	466	620	701	755	801	840	877	912	946	977	1,013	1,044								
13	17	1,035	482	610	674	724	767	801	837	870	902	931	961	990	1,022							
14	12	1,041	458	599	663	713	753	791	824	856	885	921	948	976	1,007	1,035						
15	9	1,145	500	643	718	772	818	858	899	931	962	993	1,022	1,050	1,077	1,105	1,134					
16	3	1,189	513	668	753	807	847	883	919	954	981	1,008	1,043	1,070	1,097	1,123	1,154	1,181				
17	2	1,216	504	629	708	766	811	850	889	928	960	992	1,018	1,056	1,088	1,120	1,152	1,177	1,203			
18	2	1,272	480	642	737	785	834	871	920	950	981	1,018	1,049	1,074	1,105	1,130	1,159	1,191	1,215	1,246		
19	2	1,075	416	551	626	663	704	740	766	791	812	843	869	889	916	936	962	983	1,003	1,034	1,054	
20	2	1,151	464	603	671	723	764	795	825	856	881	906	937	957	987	1,007	1,032	1,052	1,077	1,106	1,126	1,146
21	1	1,220	421	602	686	727	768	796	823	865	892	920	947	974	988	1,015	1,043	1,070	1,084	1,111	1,138	1,165	1,192
Total number			424	408	384	365	322	271	234	204	190	151	109	77	50	33	21	12	9	7	5	3	1
Weighted mean			486	635	716	772	817	852	886	917	949	975	1,002	1,017	1,032	1,064	1,110	1,118	1,120	1,126	1,100	1,152	1,192
Growth increment			486	148	81	56	45	34	34	31	31	26	26	15	15	32	46	8	2	6	−26	52	40

TABLE 4.—Mean fork lengths (mm) at capture and mean back-calculated fork lengths at ages from sectioned otoliths of king mackerel, sexes combined.

Age	No. of specimens	Mean length at capture	Mean back-calculated lengths at successive annuli																			
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	48	538	461																				
2	37	722	515	668																			
3	30	800	520	670	759																		
4	70	823	513	645	727	788																	
5	74	859	513	652	733	791	837																
6	61	871	500	635	708	763	810	851															
7	56	899	494	631	710	762	807	847	883														
8	28	938	508	650	722	773	814	850	884	918													
9	59	956	495	626	708	761	803	840	874	908	941												
10	59	976	492	636	703	758	798	836	868	900	932	963											
11	43	1,020	502	640	713	764	806	845	878	911	941	971	1,003										
12	39	1,018	479	625	697	746	788	823	855	887	916	944	974	1,002									
13	29	986	471	602	665	711	750	781	813	842	871	897	922	947	975								
14	20	1,007	464	597	662	709	747	781	812	840	868	898	922	947	974	998							
15	15	1,065	494	629	700	747	786	819	854	882	909	935	960	984	1,008	1,032	1,056						
16	6	1,068	490	610	684	738	775	806	837	867	889	914	943	966	989	1,013	1,037	1,060					
17	2	1,216	538	661	737	793	836	873	910	947	977	1,007	1,031	1,067	1,097	1,127	1,156	1,180	1,204				
18	2	1,272	516	676	767	813	860	896	942	970	1,000	1,035	1,064	1,087	1,117	1,139	1,167	1,196	1,219	1,248			
19	2	1,075	447	580	653	688	727	762	786	810	830	859	883	902	927	946	971	990	1,009	1,037	1,056		
20	2	1,151	497	633	699	748	788	817	846	875	899	923	951	970	998	1,017	1,041	1,059	1,082	1,110	1,128	1,146	
21	1	1,220	456	635	716	756	795	822	848	887	913	939	965	991	1,004	1,029	1,055	1,080	1,093	1,119	1,144	1,169	1,194
Total number			683	635	598	568	498	424	363	307	279	220	161	118	79	50	30	15	9	7	5	3	1
Weighted mean			497	638	712	763	802	833	864	892	920	943	964	975	989	1,020	1,060	1,086	1,124	1,130	1,102	1,154	1,194
Growth increment			497	141	73	51	39	30	30	28	27	23	20	11	13	31	39	26	38	5	−27	51	40

TABLE 5.—Mean fork lengths (mm) at capture and mean back-calculated fork lengths at ages from whole otoliths of male king mackerel.

Age	No. of specimens	Mean length at capture	Mean back-calculated lengths at successive annuli								
			1	2	3	4	5	6	7	8	9
1	18	505	402								
2	8	689	511	670							
3	11	758	468	654	731						
4	20	794	488	655	726	772					
5	17	821	451	642	721	764	802				
6	5	827	420	629	688	737	772	805			
7	6	847	417	642	705	745	776	806	823		
8	0	—	—	—	—	—	—	—	—	—	
9	5	896	452	625	699	741	773	797	831	853	871
Total number			90	72	64	53	33	16	11	5	5
Weighted mean			453	649	719	760	788	803	827	853	871
Growth increment			453	195	70	41	28	14	23	26	17

TABLE 6.—Mean fork lengths (mm) at capture and mean back-calculated fork lengths at ages from whole otoliths of female king mackerel.

Age	No. of specimens	Mean length at capture	Mean back-calculated lengths at successive annuli											
			1	2	3	4	5	6	7	8	9	10	11	12
1	18	552	440											
2	20	712	481	666										
3	26	810	502	696	780									
4	42	845	490	671	762	814								
5	46	882	474	670	759	820	862							
6	35	915	471	673	757	810	851	892						
7	21	949	453	651	746	802	845	887	921					
8	12	1,022	467	697	788	837	881	924	963	995				
9	8	1,035	475	669	785	842	885	918	954	986	1,018			
10	9	1,079	485	689	778	837	890	931	964	997	1,028	1,056		
11	1	1,138	350	654	785	814	873	917	976	1,020	1,064	1,093	1,123	
12	1	1,077	387	454	724	778	806	846	873	927	968	995	1,022	1,077
Total number			239	221	201	175	133	87	52	31	19	11	2	1
Weighted mean			475	673	764	817	861	901	943	992	1,022	1,054	1,073	1,077
Growth increment			475	197	91	52	44	40	42	48	30	31	18	3

Van Oosten (1929) listed assumptions involved in the use of hard parts to determine age of fish: 1) the structures used are constant in number and identity throughout the life of the fish, 2) the ratio of structure size and fish size (length) remains constant with growth, and 3) marks (rings) are annual and form at about the same time each year. The first assumption is not in doubt for otoliths. Supporting the second assumption are the correlations between fish length and otolith radius, which were significant for whole and sectioned otoliths but stronger for the latter. It is in meeting the final assumption that the validity of ages from whole otoliths becomes doubtful. The distributions of focus-ring measurements were only slightly better for sectioned than for whole otoliths. However, the distribution of monthly percentages of whole otoliths with opaque margins was multimodal, indicating nonannual ring formation (or large and numerous reading errors), while that of sections was unimodal and fairly normal, indicating annual ring formation peaking in August–September. Manooch et al. (1987) found a peak in ring formation during February–May, but they also found ring formation in September for some fish taken off northwest Florida and suggested that this difference may be due to separate spawning groups within the Gulf of Mexico.

We consider rings in otolith sections valid annuli, but our evidence for validation is indirect, as in previous studies of king mackerel. As pointed out

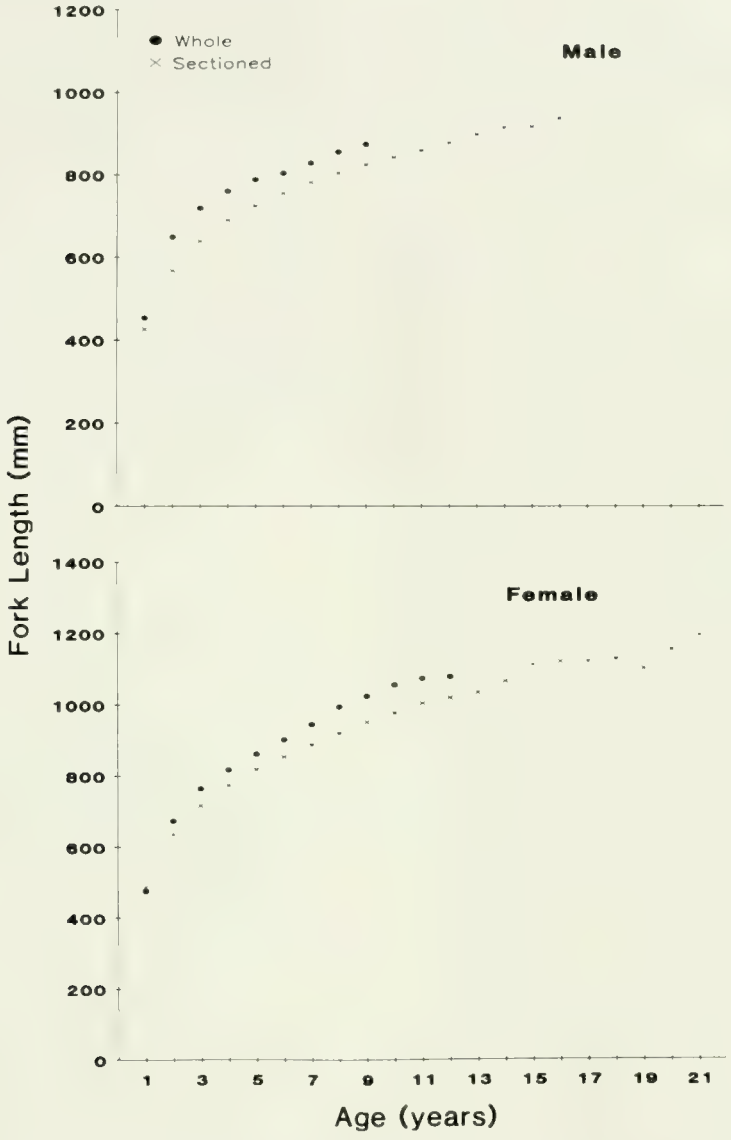

FIGURE 6.—Mean back-calculated lengths at age from whole and from sectioned otoliths for male and female king mackerel.

by Van Oosten (1929) and restated by Beamish and McFarlane (1983), procedures that produce direct evidence and validate ages of all age groups include mark-recapture techniques (which will involve chemical labeling if ages are to be determined from otoliths) and capture of known-age fish. The only previous study of king mackerel producing acceptable evidence for age validation (Manooch et al. 1987) generated very different life history characteristics from ours, including maximum ages of 11 and 14 for males and females, respectively, but was based on whole otoliths from Gulf of Mexico fish. Thus, whether the differing results are due to separate groups of king mackerel with different life history characteristics or to differences in techniques is not known. Regardless, we have demonstrated that dubious information from whole otoliths can appear valid, and suggest that sectioned sagittae be used to age king mackerel in future studies.

TABLE 7.—Mean fork lengths (mm) at capture and mean back-calculated fork lengths at ages from whole otoliths of king mackerel, sexes combined.

Age	No. of specimens	Mean length at capture	Mean back-calculated lengths at successive annuli											
			1	2	3	4	5	6	7	8	9	10	11	12
1	46	532	396											
2	30	706	453	662										
3	47	793	439	656	755									
4	69	827	437	635	734	792								
5	64	866	412	626	727	794	843							
6	44	898	410	629	721	780	827	872						
7	27	926	385	606	704	764	812	858	894					
8	13	1,014	404	644	749	803	853	902	947	983				
9	14	985	406	602	711	770	816	853	895	927	960			
10	9	1,079	421	636	734	800	861	907	945	983	1,019	1,052		
11	1	1,138	285	593	736	768	833	883	950	1,000	1,051	1,086	1,120	
12	1	1,077	322	390	675	735	765	811	841	903	950	981	1,013	1,077
	Total number		365	319	289	242	173	109	65	38	25	11	2	1
	Weighted mean		418	633	730	786	833	872	912	961	984	1,048	1,067	1,077
	Growth increment		418	215	96	56	46	39	39	48	23	63	18	9

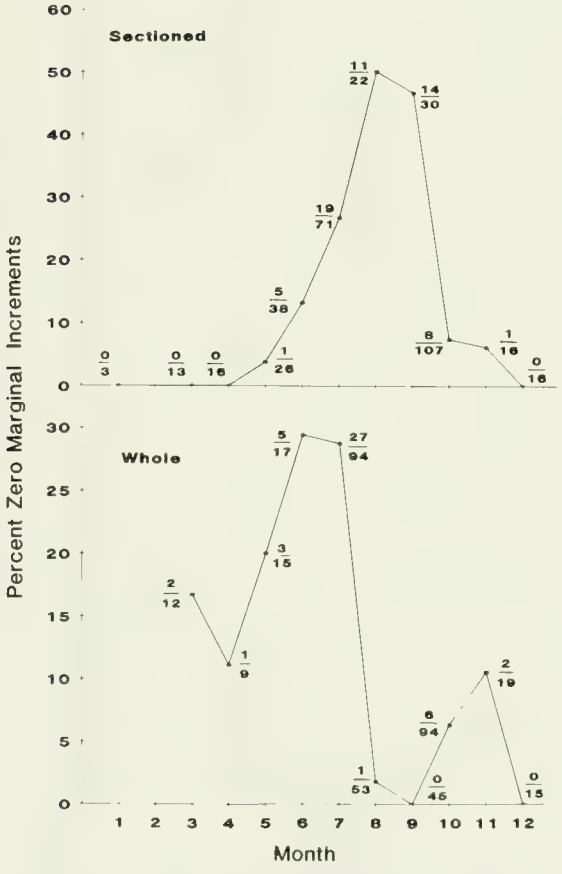

FIGURE 7.—Monthly percentages of zero marginal increments on whole and sectioned otoliths, with number of zero marginal increments over number in sample for each month.

TABLE 8.—von Bertalanffy growth parameters from whole and from sectioned otoliths of king mackerel.

Sex	Parameter	Estimate	Asymptotic 95% confidence interval	
			Lower	Upper
Sectioned otoliths				
Male	L_∞	942	905	979
	K	0.1915	0.1471	0.2358
	t_0	−2.5006	−3.4139	−1.5874
Female	L_∞	1,208	1,156	1,260
	K	0.1239	0.0978	0.1500
	t_0	−3.7445	−4.8442	−2.6448
Combined	L_∞	1,277	1,162	1,392
	K	0.0872	0.0572	0.1172
	t_0	−5.6836	−7.7409	−3.6262
Whole otoliths				
Male	L_∞	853	816	889
	K	0.5170	0.3334	0.7006
	t_0	−0.5266	−1.1493	−0.0960
Female	L_∞	1,122	1,051	1,192
	K	0.2278	0.1570	0.2987
	t_0	−1.6572	−2.5360	−0.7784
Combined	L_∞	1,127	1,027	1,227
	K	0.2128	0.1304	0.2951
	t_0	−1.4777	−2.5008	−0.4546

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EFFECTS OF FOOD CONCENTRATION AND TEMPERATURE ON DEVELOPMENT, GROWTH, AND SURVIVAL OF WHITE PERCH, *MORONE AMERICANA*, EGGS AND LARVAE

DANIEL MARGULIES[1]

ABSTRACT

Growth and mortality during the egg and early larval stages of white perch, *Morone americana*, were examined in relation to food concentration and temperature. Laboratory experiments were conducted utilizing variable food conditions (high, low, and initially delayed rotifer levels) and temperatures (13°, 17°, and 21°C). Egg and yolk-sac larva stage durations were inversely related to temperature, and optimum hatch of eggs occurred at 17°C or lower. Larvae fed initially at low food levels for as little as 2 days exhibited significantly reduced survival and growth after 8 days of feeding at all temperatures. Survival rates of well-fed larvae after 8 days of feeding ranged from 43 to 55%. Feeding delays of 4–8 days resulted in markedly reduced survival at 17° and 21°C. Growth was slow under any food conditions at 13°C (<0.05 mm/d in length, <5%/d in dry weight). At 17° and 21°C, well-fed larvae grew at significantly higher rates (>0.20 mm/d in length, >15%/d in dry weight). Based on these laboratory data and on seasonal abundance of food in Chesapeake tributaries, it was estimated that optimum temperatures for growth and survival of first-feeding white perch larvae are 15°–20°C. Results suggest that the estimation of variability in growth rates of larval white perch in Chesapeake tributaries would make a major contribution to our understanding of white perch recruitment.

The white perch, *Morone americana*, is an important recreational and commercial fish species in the Chesapeake Bay drainage. Fluctuations in relative abundance of white perch are most likely related to survivorship during the early life history, yet surprisingly little is known about the effects of varying environmental factors on growth, development, and survival of white perch eggs and larvae.

Past studies on the early life history of white perch have focused on distribution patterns (Mansueti 1961), descriptions of egg and larval development (Mansueti 1964), electrophoretic (Morgan 1975), and biochemical (Sidell and Otto 1978) characterizations of larvae and temperature effects on hatching (Morgan and Rasin 1982). The interacting effects of temperature and food on the development, growth, and survival of white perch eggs and larvae had not been studied previously.

Fecundity of white perch, which usually are 100–250 mm SL, is high (50,000–300,000 ova per female), thus larval mortality rates are expected to be high (Ware 1975). For most high-fecundity species, if large numbers of larvae are produced in a cohort, small changes in growth or mortality rates during the larval stages may produce large variations in recruitment (Houde 1987). White perch juveniles are large relative to reproductive size, with the greatest relative weight increases occurring in the larval stage. This growth pattern indicates a strong potential for regulation of numbers through variable larval growth (Houde 1987).

In this study, I examined the effects of two variable environmental factors, food concentration and temperature, on the development, growth, and survival of first-feeding white perch larvae. White perch spawn in Chesapeake tributaries over a temperature range of 10°–20°C (Hardy 1978). Thus, first-feeding larvae can encounter a wide range of developmental temperatures. Microzooplankton, which forms the bulk of the diet for first-feeding white perch larvae, can fluctuate in Chesapeake tidal freshwaters during spring months from <50 to >1,000/L (Heinle and Flemer 1975; Lippson et al. 1980). By examining the interacting effects of temperature and food, the scope for growth and survival potential of white perch larvae were studied.

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METHODS

Experimental Design

White perch adults were collected by otter trawl from the Potomac and Patuxent Rivers, MD during April and May 1982. Eggs were collected from at least four females and milt from four males from each river system. Gametes were stripped into 8 L polycarbonate containers. Fertilized eggs were then transported to the laboratory and placed in well-aerated, 38 L tanks divided into three temperature groups: 13°, 17°, and 21°C. Salinity was maintained at 1‰. After hatching, yolk-sac larvae were transferred to 38 L culture tanks. Feeding studies were initiated with larvae that had some yolk remaining and which had pigmented eyes, indicating readiness to initiate feeding (Blaxter 1969).

All feeding experiments were conducted for a period of 8 days. Partial water changes of 25% were made in each feeding tank every other day to minimize buildup of metabolites. Fluorescent lighting provided constant 200–300 lux, with photoperiod maintained on a 13 h light: 11 h dark cycle. Temperature was controlled to the nearest 0.5°C by maintaining aquaria in water baths of ambient Patuxent River water and regulating individual tanks by aquarium heaters.

Food for larvae consisted of rotifers (*Brachionus plicatilis*) cultured in the laboratory on the green alga *Chlorella* sp. Field studies demonstrated that *Brachionus* constitutes the bulk of the diet of first-feeding white perch larvae (Martin and Setzler-Hamilton 1983). Based on a size analysis of zooplankton prey consumed by Potomac River larvae, rotifers were graded as follows: Day 1 to day 3: 100–150 μm in breadth provided; and day 4 to day 8: all sizes (100–180 μm) provided. Food levels were measured in the feeding tanks by calculating the mean values of three 100 mL aliquots taken four times daily. Food concentrations subsequently were adjusted to nominal levels.

Four food groups were established, representative of high, low, and delayed-high food conditions. Group 1 was a well-fed group maintained at 800 rotifers/L; group 2 was maintained at 50 rotifers/L concentrations for 2 days and then fed at 800 rotifers/L levels for 6 days; group 3 was fed at 50 rotifers/L levels for 4 days and then fed at 800 rotifers/L concentrations for 4 days; group 4 was maintained at low levels of 50 rotifers/L for the entire study period. The food levels of 800 and 50 rotifers/L were representative of high and low microzooplankton levels that typically occur in tidal freshwaters of the Chesapeake (Lippson et al. 1980).

Each food group was tested at three temperatures: 13°, 17°, and 21°C. At each temperature, 10 eggs and 10 newly hatched larvae were sampled from the rearing tanks and fixed in 4% formalin to test for possible incubation temperature or parental stock effects on egg and newly hatched larva sizes. Just prior to feeding, 10 larvae were removed from each temperature stock tank and preserved for initial length and dry weight measurements.

At each temperature, 150 larvae were assigned to each of two replicates for each food group (with four food groups per temperature). Once feeding was initiated, at 2 d intervals, subsamples of 3 or 4 larvae were removed from each tank and preserved in 4% formalin for growth analyses.

Sample Analyses

Mean egg diameter, larval hatching length, and length at first-feeding were measured and compared among temperatures. Yolk and oil globule dimensions of eggs and larvae were measured by ocular micrometer and converted to yolk and oil volumes (mm^3); the stage-specific volumes were then compared among temperatures. Regressions also were developed predicting the duration of the egg and yolk-sac stages in relation to temperature.

Expected mean survival after 8 days of feeding was calculated based on the relationship: $N_t = N_0 e^{-Zt}$, where N_t = number of survivors at t days after first-feeding (8 days), N_0 = initial number of larvae (150), t = number of days of feeding (8), and Z = instantaneous total mortality rate. Also, $Z = F + M$, where F = sampling mortality and M = natural mortality rate. The number of larvae preserved for analyses was considered sampling mortality (F), and all other mortality was M. Thus, when N_0, N_t, t, Z, and F were known, it was possible to solve for M, from which expected number of survivors was calculated as N_t (Expected) = $N_0 e^{-Mt}$ (Ricker 1975).

Growth rates were calculated from the subsamples of preserved larvae. Lengths were measured after three weeks of preservation using a Wild[2] dissecting microscope fitted with an ocular micrometer. Lengths were recorded to the nearest 0.1 mm. Dry weight was obtained by drying larvae at 60°C for 48 hours, dessicating, and weighing to the nearest 0.1 μg on a Cahn electrobalance. Growth in length was estimated by linear regression: $L_t = a$

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

$+ bt$, where L_t is length at time "t" days and b is daily growth rate (mm per day). Growth in weight for the 8 d period was determined from the exponential regression of dry weight on days after first-feeding: $W_t = W_0 e^{Gt}$, where W_t = dry weight at time "t" days, G = instantaneous daily growth coefficient, and W_0 = dry weight at first-feeding. Specific growth rate (percent per day) was calculated as $100(e^G - 1)$. In addition, mean incremental growth coefficients (i.e., between sampling days 2, 4, 6, and 8) also were calculated (Ricker 1975).

Data were analyzed by regression analysis, analysis of variance (ANOVA), and analysis of covariance (ANCOVA) followed by the Student-Newman-Kuels (SNK) multiple comparison test (Sokal and Rohlf 1981). The probability level for rejecting null hypotheses was $P = 0.05$.

RESULTS

Development

Preserved white perch eggs ranged from 0.76 to 1.03 mm in diameter. Mean diameters of eggs hatched at 13°, 17°, and 21°C were 0.91, 0.87, and 0.92 mm, respectively (Table 1). Each egg contained a large volume of yolk (0.14–0.16 mm^3), and a prominent, amber-colored oil globule (0.0070–0.0081 mm^3). There were no significant differences (ANOVA, $P > 0.10$) among incubation temperatures for mean egg diameter, yolk volume, or oil globule volume (Table 1).

TABLE 1.—Characteristics of fertilized white perch eggs, newly hatched larvae and first-feeding larvae cultured at three temperatures.

	Temperature (°C)		
	13	17	21
Parameter n:	10	10	10
Eggs			
$\bar{x}$ diameter (mm)	0.91	0.87	0.92
$SE_{\bar{x}}$	0.02	0.02	0.03
$\bar{x}$ yolk vol (mm^3)	0.14	0.15	0.16
$SE_{\bar{x}}$	0.01	0.01	0.01
$\bar{x}$ oil glob. vol (mm^3)	0.0081	0.0070	0.0080
$SE_{\bar{x}}$	0.0005	0.0004	0.0004
Newly hatched larvae			
$\bar{x}$ SL (mm)	2.52	2.46	2.53
$SE_{\bar{x}}$	0.03	0.03	0.02
$\bar{x}$ dry wt (μg)	35.2	34.0	36.4
$SE_{\bar{x}}$	1.3	1.1	1.2
First-feeding larvae			
$\bar{x}$ SL (mm)	3.48	3.43	3.49
$SE_{\bar{x}}$	0.06	0.05	0.05
$\bar{x}$ dry wt (μg)	18.8	18.4	19.4
$SE_{\bar{x}}$	0.5	0.4	0.6
$\bar{x}$ yolk vol (mm^3)	0.0026	0.0018	0.0014
$SE_{\bar{x}}$	0.0005	0.0004	0.0004
$\bar{x}$ % yolk remaining	1.87	1.53	0.75
$SE_{\bar{x}}$	0.36	0.33	0.23
$\bar{x}$ oil glob. vol (mm^3)	0.0036	0.0023	0.0022
$SE_{\bar{x}}$	0.0007	0.0003	0.0006
$\bar{x}$ % oil remaining	44.1	32.1	27.6
$SE_{\bar{x}}$	7.8	4.6	7.0

Mean larval size at hatch ranged from 2.37 to 2.81 mm SL and averaged 2.50 mm (Table 1). Dry weight of hatchlings was approximately 35 μg. Newly hatched larvae had unpigmented eyes, with the head deflected downward over the yolk sac. Mean lengths and weights of newly hatched larvae at the three temperatures did not differ significantly (ANOVA, $P > 0.10$).

At the first-feeding stage, larvae averaged 3.45 mm SL and weighed approximately 19 μg (Table 1). First-feeding larvae had utilized at least 98% of their yolk reserves and from 55 to 75% of their oil. At the first-feeding stage no significant temperature effects were apparent for size of larvae, percentage of yolk remaining or percentage of oil volume remaining (ANOVA, $P > 0.10$). Although not significant, there was a trend for larvae to retain more yolk and oil at lower temperatures.

Temperature had a pronounced effect on the duration of the egg and yolk-sac larval stages (Fig. 1). The relationships between the durations of these stages and temperature were best described by decreasing exponential functions. Although effect of temperature on hatching success was not measured precisely, rough estimates based on removals of dead eggs were made. Percentage hatch was near 80% at 13°C, approximately 60% at 17°C, and near 20% at 21°C.

Survival

Expected survival after 8 days of feeding ranged from 4.0 to 55.0%, depending on temperature and food conditions (Fig. 2). As expected, survival at each temperature was highest for the well-fed larvae in food group 1. Larvae fed at low food levels for as little as 2 days (groups 2, 3, and 4) exhibited significantly reduced survival at all temperatures (ANOVA and SNK procedure, $P < 0.05$). In particular, larvae fed at low food concentrations for 4–8 days (groups 3 and 4) displayed markedly reduced survival at 17° and 21°C.

Growth

At 13°C, growth in length was slow under all food conditions—all larvae were <4.0 mm SL after 8 days

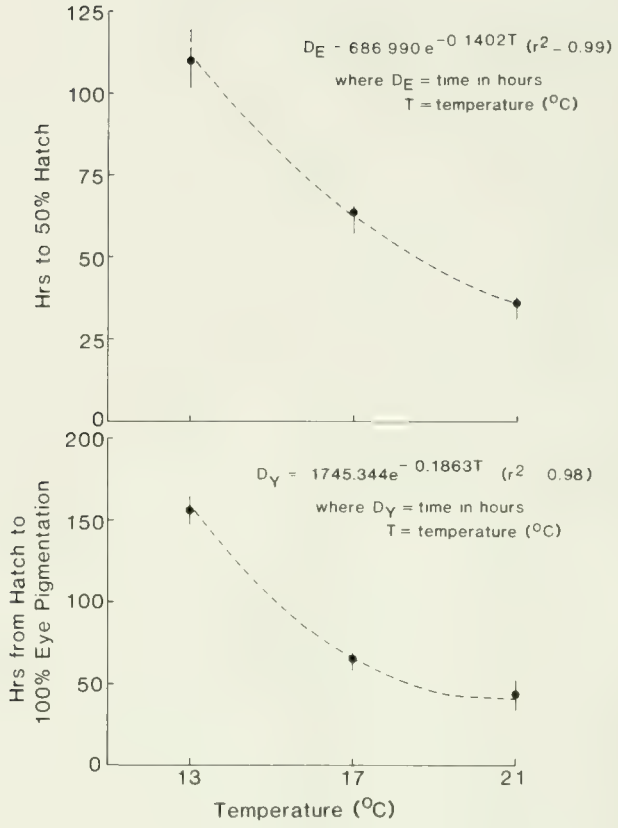

FIGURE 1.—The effect of temperature on egg and yolk-sac stage duration of white perch. Plotted values are means ±2 SE.

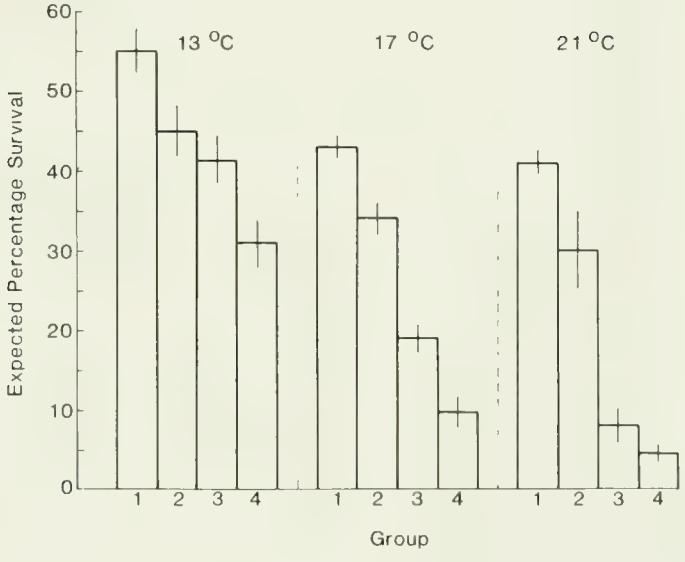

FIGURE 2.—Mean expected survival of white perch larvae after eight days of feeding. Error bars are ±2 SE.

(Fig. 3). At 17° and 21°C, food level effects were clearly demonstrated and the final lengths attained by larvae in all food groups differed significantly from each other (SNK procedure, $P < 0.05$). The well-fed larvae in groups 1 and 2 were significantly longer after 8 days of feeding at 17° and 21° than they were at 13° (SNK procedure, $P < 0.05$).

Depending on food and temperature conditions, larvae grew in length at rates ranging from 0.01 to 0.28 mm/d (Table 2). The larvae in group 1 exhibited the highest growth rate at all temperatures, growing at 0.05 mm/d at 13°C, 0.20 mm/d at 17°C, and 0.28 mm/d at 21°C. At 17° and 21°C, larvae in groups 1 and 2 grew significantly faster than those in groups 3 or 4 (ANCOVA and SNK procedure, $P < 0.05$). For either group 1 or 2, an increase in temperature resulted in a significantly higher growth rate compared to 13°C (SNK procedure, $P < 0.05$). The linear regressions gave good fits to the growth-in-length data, although there was some indication that growth at 17° and 21°C for groups 1 and 2 was becoming more curvilinear after day 4 (Table 2, Fig. 3).

Well-fed larvae (group 1) were significantly heavier at all three temperatures (ANOVA and SNK procedure, $P < 0.05$). At 17° and 21°C, final mean weights of larvae from all food groups differed significantly from each other (SNK procedure, $P < 0.05$). As temperature increased, weight increases were most pronounced for groups 1 and 2 (Fig. 4).

The well-fed group 1 larvae had the highest

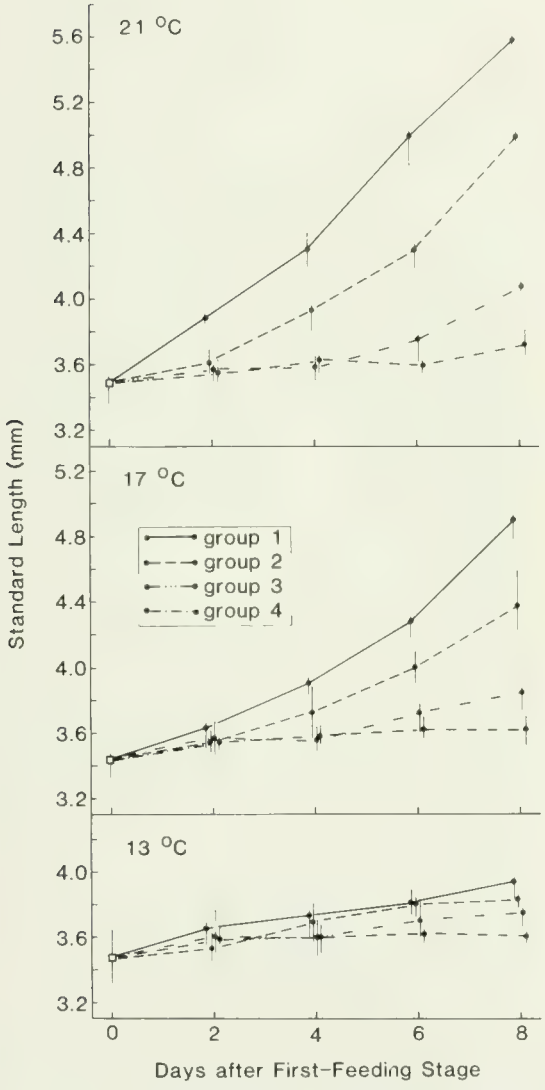

FIGURE 3.—Growth in standard length of white perch larvae tested under four food availability conditions and at three temperatures. Plotted values are means ±2 SE.

TABLE 2.—Regression equations describing growth in length of white perch larvae tested under four food availability conditions and at three temperatures. Feeding duration was 8 days. In the regression equation, L is standard length in mm, t equals days after first-feeding, b is growth rate in mm, and a is the y-intercept. Results of ANCOVA and multiple comparison procedures (SNK) also are given.

T (°C)	Food group	n	Regression equation	SE_b	r^2
13	1	40	$L = 3.546 + 0.054t$	0.004	0.97
	2	42	$L = 3.465 + 0.049t$	0.005	0.96
	3	41	$L = 3.511 + 0.029t$	0.006	0.91
	4	41	$L = 3.550 + 0.013t$	0.007	0.57
17	1	39	$L = 3.176 + 0.202t$	0.024	0.95
	2	39	$L = 3.250 + 0.133t$	0.015	0.95
	3	37	$L = 3.418 + 0.050t$	0.007	0.94
	4	40	$L = 3.521 + 0.014t$	0.006	0.77
21	1	38	$L = 3.293 + 0.276t$	0.019	0.97
	2	40	$L = 3.143 + 0.216t$	0.029	0.93
	3	35	$L = 3.381 + 0.073t$	0.011	0.94
	4	38	$L = 3.523 + 0.020t$	0.006	0.86

ANCOVA result: The growth rates differ significantly ($P < 0.001$).

SNK summary (different superscript numbers on each line indicate significant differences among growth rates ($P < 0.05$)):

Among food groups (FG):

(°C)	FG1	FG2	FG3	FG4
13	0.054^{1}	$0.049^{1,2}$	$0.029^{2,3}$	0.013^{3}
17	0.202^{1}	0.133^{2}	0.050^{3}	0.014^{4}
21	0.276^{1}	0.216^{1}	0.073^{2}	0.020^{3}

Among temperatures:

Food group	13°	17°	21°
1	0.054^{1}	0.202^{2}	0.276^{3}
2	0.049^{1}	0.133^{2}	0.216^{3}
3	0.029^{1}	$0.050^{1,2}$	0.073^{2}
4	0.013^{1}	0.014^{1}	0.020^{1}

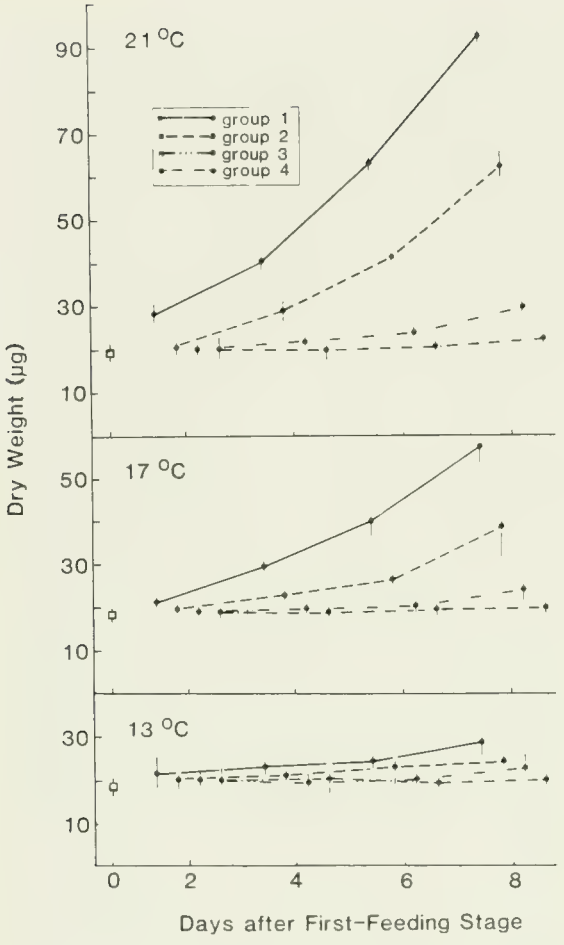

FIGURE 4.—Growth in dry weight of white perch larvae tested under four food availability conditions and at three temperatures. Plotted values are means ±2 SE.

TABLE 3.—Regression equations describing growth in weight of white perch larvae tested under four food availability conditions and at three temperatures. Feeding duration was 8 days. In the regression equation, W is dry weight in µg, t equals days after first-feeding, G is the instantaneous growth coefficient, and W_0 is dry weight at time 0. Results of ANCOVA and multiple comparison procedures (SNK) also are given.

T (°C)	Food group	n	Regression equation	SE_G	r^2	Percent gain (% d^{-1})
13	1	40	$W = 19.029\ e^{0.0481t}$	0.0062	0.96	4.9
	2	42	$W = 18.774\ e^{0.0328t}$	0.0020	0.98	3.3
	3	41	$W = 18.911\ e^{0.0196t}$	0.0076	0.68	2.0
	4	41	$W = 19.433\ e^{0.0058t}$	0.0054	0.24	0.6
17	1	39	$W = 18.938\ e^{0.1413t}$	0.0095	0.98	15.2
	2	39	$W = 16.910\ e^{0.1084t}$	0.0178	0.91	11.4
	3	37	$W = 18.099\ e^{0.0317t}$	0.0068	0.88	3.2
	4	40	$W = 18.858\ e^{0.0089t}$	0.0037	0.66	0.9
21	1	38	$W = 19.254\ e^{0.1973t}$	0.0101	0.99	21.8
	2	40	$W = 19.298\ e^{0.1436t}$	0.0158	0.96	15.4
	3	35	$W = 18.216\ e^{0.0538t}$	0.0106	0.89	5.5
	4	38	$W = 19.497\ e^{0.0147t}$	0.0050	0.73	1.5

ANCOVA result: The growth rates differ significantly ($P < 0.001$).

SNK summary (different superscript numbers on each line indicate significant differences among growth rates ($P < 0.05$)):

Among food groups (FG):

(°C)	FG1	FG2	FG3	FG4
13	0.0481^{1}	$0.0328^{1,2}$	$0.0196^{2,3}$	0.0058^{3}
17	0.1413^{1}	0.1084^{2}	0.0317^{3}	0.0089^{3}
21	0.1973^{1}	0.1436^{2}	0.0538^{3}	0.0147^{4}

Among temperatures:

Food group	13°	17°	21°
1	0.0481^{1}	0.1413^{2}	0.1973^{3}
2	0.0328^{1}	0.1084^{2}	0.1436^{2}
3	0.0196^{1}	$0.0317^{1,2}$	0.0538^{2}
4	0.0058^{1}	0.0089^{1}	0.0147^{1}

growth rates at all temperatures (Table 3). At 17° and 21°C group 2 larvae, delayed only 2 days, had significantly reduced overall weight gains compared to group 1 larvae (ANCOVA and SNK procedure, $P < 0.05$). Weight gains after 8 days for groups 3 and 4 were significantly lower at all temperatures (SNK procedure, $P < 0.05$) (Table 3).

The mean instantaneous growth rates attained by larvae at 2 d intervals showed several important patterns (Fig. 5). At all temperatures, feeding at 800 versus 50 rotifer/L food levels produced significantly different growth rates in 2 days or less (ANOVA, $P < 0.05$). At 13°C, growth differences among food groups were established after 2 days but became inconsistent, while food group differences became more pronounced at higher temperatures. At 17° and 21°C, larvae that had 2 d delays before being offered the high food level (group 2) equalled group 1 growth rates after lag times of 2–4 days. Growth recoveries from 4 d delays were slower and incomplete, but there were strong indications that group 3 larvae were initiating substantial growth during the last 2 days of feeding. Group 4 larvae lost weight from day 2 to day 4 and grew slowly throughout the study.

Instantaneous growth coefficient also was regressed on temperature for each food group (Fig. 6). All four regression coefficients (slopes) differed significantly among food groups (ANCOVA with SNK procedure, $P < 0.05$). Growth rates of all food groups diverged at a faster rate in the upper half of the temperature range. Growth coefficients for groups 1 and 2 larvae increased by factors of 3.5–4.0 within the temperature range tested (13°–21°C).

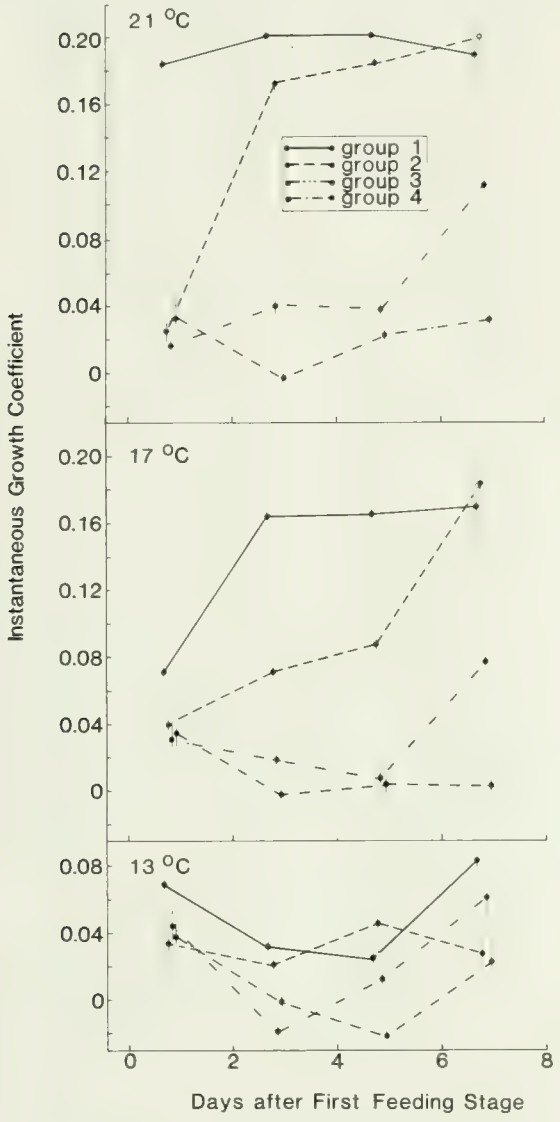

FIGURE 5.—Mean instantaneous growth coefficients attained by white perch larvae at 2 d intervals. Error bars are ±2 SE.

DISCUSSION

White perch produce large numbers of eggs, hatch at small sizes (<3 mm) and undergo pronounced differences in development, growth, and survival in relation to variable food and temperature conditions. Egg stage duration decreased by a factor of three over the temperature range of 13°–21°C, but the reduced duration at higher temperatures was offset by a decline in percent hatch of nearly 60%. Morgan and Rasin (1982) reported that optimum hatch of white perch eggs in the laboratory occurred at 14°–16°C, and believed that greater percent hatch occurred in the estuary at these temperatures. Hardy (1978) reported that peak spawning activity for Chesapeake Bay white perch occurs at 12°–16°C. My results indicate that optimum temperatures for hatch occur at ≤17°C.

The effect of temperature on yolk-sac stage duration may be important. Prolongation of this stage could have significant effects on cohort survival. Predation by planktivorous fishes on yolk-sac larvae is probably substantial in tidal freshwaters, based on the results of laboratory predation experiments (Margulies 1986). Results reported here indicate that a short-term decrease in temperature of 4°C during the spawning season, which is not unusual in tidal freshwaters (James et al. 1984[3]), could prolong the yolk-sac stage by at least 3 days, which could

[3]James, R. W., R. H. Simmons, and B. F. Strain. 1984. Water resources data, Maryland and Delaware, Water Year 1983. U.S. Geol. Surv. Water-Data Rep. MD-DE-83-1.

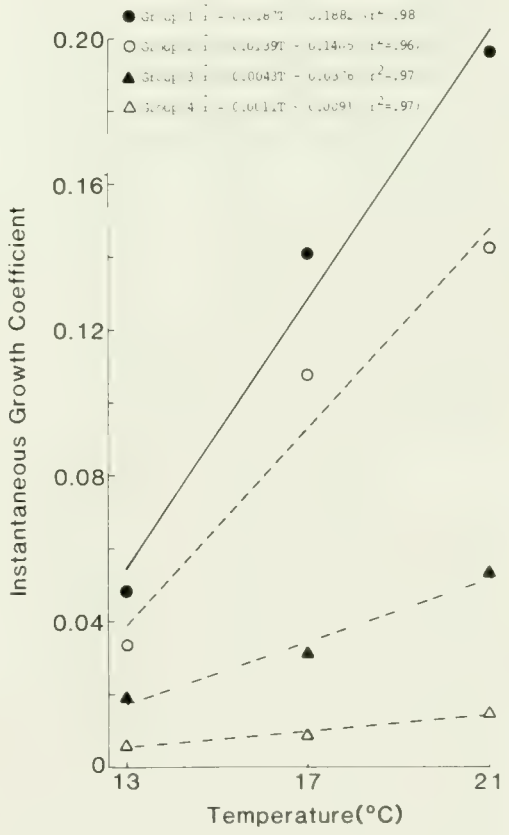

FIGURE 6.—Relationship between temperature and instantaneous growth coefficient for each food group.

substantially increase larval mortality due to fish predation.

Survival of white perch larvae is strongly dependent upon food availability and temperature. At 13°C, larvae were vulnerable to low food conditions, but survival differences after 8 days among malnourished and well-fed larvae were much more pronounced at higher temperatures. The metabolic demands of larvae are reduced at low temperatures, allowing relatively low caloric intake to sustain larvae. The food levels of 800 and 50 rotifers/L used in the study correspond to caloric values of 0.64 and 0.04 cal/L, respectively (Theilacker and McMaster 1971). It was apparent from survival data, particularly at 17° and 21°C, that 0.04 cal/L was inadequate for white perch survival, and that critical levels for survival fall in the range of 0.04–0.64 cal/L. This estimate falls within the broad range of 0.01 to 10.0 cal/L that Houde (1978) summarized as reported critical caloric concentrations for marine fish larvae.

White perch resemble many small marine and estuarine larvae (e.g., northern anchovy, *Engraulis mordax*; jack mackerel, *Trachurus symmetricus*; spot, *Leiostomus xanthurus*) in having relatively low survival potential at low food levels (Theilacker and Dorsey 1980; Powell and Chester 1985). For example, at 17° and 21°C, 8 d survival values for white perch decreased by 60–80% with a 4 d delay in high food levels. At those same temperatures, an 8 d delay resulted in 80–90% decreases in survival. Larger larvae such as sand lance, *Ammodytes americanus*, (Buckley et al. 1984); Atlantic herring, *Clupea harengus harengus*, (Rosenthal and Hempel 1970; Kiorboe and Munk 1986); and striped bass, *Morone saxatilis*, (Houde and Lubbers 1986) are less vulnerable to starvation under low-food conditions. When food is scarce, smaller larvae such as white perch are often more vulnerable to starvation because of low frequency of prey contact (Laurence 1982). However, comparisons among species should be done with caution because survival potential is species-specific. For example, sea bream, *Archosargus rhomboidalis*, (Houde 1978); plaice, *Pleuronetes platessa*, (Blaxter and Staines 1971); and cod, *Gadus morhua*, (Ellertsen et al. 1981), all relatively small at first-feeding, are efficient feeders and exhibit significant survival at low prey levels (<50/L).

For most species, larval growth variability and stage durations are important aspects of prerecruit survival (Cushing 1976; Houde 1987). Temperature variability resulted in more than fourfold differences in mean weights of white perch larvae after 8 days of feeding. Thus, the effect of temperature on feeding stage duration would be even more pronounced than its effects on yolk-sac stage duration. Under good feeding conditions, a drop in temperature of 2° (from 17° to 15°, for example) would result in a 30% reduction in growth after 8 days (see Figure 6). The magnitude of the prolongation of stage duration would be similar. The effects of reduced food on stage duration would be even more pronounced. At 17° or 21°C, food levels need only be reduced for 2 days upon initiation of feeding to produce the same 30% reduction in growth after 8 days (Fig. 6).

The growth potential of white perch is intermediate between that reported for temperate and subtropical marine and estuarine species (Houde and Schekter 1981). White perch growth at 17°C and higher exceeded that reported for most temperate latitude species, which usually grow at rates of 10%/d or less (Houde and Schekter 1981). However, white perch growth rates were less than that of most subtropical species, such as bay anchovy, *Anchoa mitchilli*, (Florida populations); lined sole, *Archirus lineatus*; sea bream (Houde and Schekter 1981); and tidewater silverside, *Menidia peninsulae*, (McMullen and Middaugh 1985), which may grow at ≥20%/d. The specific growth rates of white perch larvae also appear to be slightly lower than those of the larger larvae of congeneric striped bass (Chesney 1986; Houde and Lubbers 1986).

Springtime densities of microzooplankton in Chesapeake tidal freshwaters usually begin to increase when temperatures reach 14° and peak at 20°–22°C (Lippson et al. 1980; Martin and Setzler-Hamilton 1981). Temperature and food concentration have important interacting effects on white perch during the first 2–3 weeks of life, with an apparent balance struck between hatching success, growth rate, and survival potential. Based on my results and historical patterns of zooplankton abundance, the optimum temperatures for white perch development and growth are in the range 15°–20°C. Hatching success was optimal at ≤17°C. Larvae hatched at 13°C were not as vulnerable to starvation, but they grew at <5%/d regardless of food level. At temperatures above 17°C, larvae could grow at ≥20%/d if high food levels were available at first-feeding. However, at 21°C (and presumably at higher temperatures), hatching success declined and there was greater likelihood of starvation under suboptimum food conditions.

Ultimate survival of white perch larvae and potential for recruitment will depend on environmental conditions in the estuary and how they effect subtle changes in growth and mortality rates of prerecruit

stages. A study of larval growth patterns in Chesapeake tributaries would be useful to understand early survivorship and establishment of year-class strength in white perch. Field estimates of growth rates of white perch larvae could be compared with indices of juvenile abundance that are now obtained in Chesapeake tributaries by the Maryland Department of Natural Resources. Results of the current study indicate that even short-term variations in food and temperature can result in significant changes in survival and growth of white perch eggs and larvae.

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ESTIMATING SOME EARLY LIFE HISTORY PARAMETERS IN A TROPICAL CLUPEID, *HERKLOTSICHTHYS CASTELNAUI*, FROM DAILY GROWTH INCREMENTS IN OTOLITHS[1]

SIMON R. THORROLD[2]

ABSTRACT

Growth increments in otoliths were used to estimate the age of larval *Herklotsichthys castelnaui*, a tropical clupeid, collected from Townsville, northeastern Australia, in spring/summer of 1987. Daily periodicity of increment formation was confirmed by treating larvae with tetracycline and examining otoliths after a known time period. Initial increments were assumed to form at hatching; ages were thus minimum estimates.

Laird-Gompertz and von Bertalanffy growth models fitted the resultant length-at-age data equally well; therefore, only the Laird-Gompertz model is presented. Specific growth rates declined from 7.4% of standard length per day at 4–5 days old to 0.4% of standard length per day at metamorphosis, 45–50 days after hatching. Absolute growth rates also declined, from 0.6 mm per day at 4–5 days to 0.08 mm per day at 44–45 days. Initial absolute growth rates are as high as any reported for clupeid larvae in the field; after this initial burst, however, the growth trajectory appeared similar to those reported for herring and pilchard larvae in temperate waters.

Spawning periodicity of *H. castelnaui* during the sampling period was determined by examining temporal distribution of birthdates from otolith-aged larvae. There was indication of semilunar peaks in spawning activity, apparently associated with quarter moon phases.

A central problem in fisheries research is understanding mechanisms determining year-class strength. Evidence suggests that regulation of year classes occurs during the early life history of most fish species (Parrish 1973; Smith 1985), and attempts to account for recruitment variability have focussed on this period of the life cycle (e.g., Hjort 1914; Cushing 1975; Koslow et al. 1987). Growth has been established as a critical parameter in the survival and subsequent recruitment of larval marine fishes (Houde 1987). Weight gains of orders of magnitude during larval life suggest a potential for extremely variable growth trajectories which may be reflected in a concomitant variability in survivorship. Growth rates are intrinsically related to susceptibility to both starvation (Lasker 1981) and predation (Rothschild and Rooth 1982). Small changes in growth rate can also have a dramatic effect on recruitment by determining stage durations over which high mortality indices may operate (Houde 1987).

Length-frequency methods have been used extensively to estimate growth in larval fishes, but growth curves generated by this technique may be biased by age- and cohort-specific changes in growth rates (Crecco et al. 1983). Protracted spawning seasons may further complicate growth estimates because of the difficulties associated with connecting length modes in polymodal length-frequency distributions (Lough et al. 1982). Modal progression can also only provide mean growth estimates for larval populations. These estimates are often averaged over months or years, whereas the relevant temporal scale for critical life history events may be hours or days (Fortier and Leggett 1985).

The accuracy and precision of growth estimates for larval fishes have been greatly enhanced by the discovery of daily incremental rings in the otoliths of some fishes (Pannella 1971; see Campana and Neilson 1985; Jones 1986 for recent reviews). Ageing by counting otolith growth increments allows a direct measure of length-at-age for calculation of growth curves and may provide information on individual age and growth rates. Growth estimates have been obtained from a variety of species in this manner (e.g., Struthsaker and Uchiyama 1976; Methot and Kramer 1979). Back-calculation of daily rings may reveal temporal distribution of birthdates (Townsend and Graham 1981; Methot 1983), and

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has allowed both temporal and spatial variability in daily growth rates to be investigated (Graham and Townsend 1985; Thomas 1986; Leak and Houde 1987).

Although temperate clupeid species have been the focus of considerable scientific attention (Blaxter and Hunter 1982), the diverse assemblage of heavily exploited clupeids of the tropical Indo-Pacific remain poorly understood (Longhurst 1971; Whitehead 1985). There is a limited selection of literature available on the Indian oil sardines (*Sardinella aurita* and *S. longiceps* (e.g., Nair 1959; Raja 1970)), but these species are not a conspicuous component of nearshore fish communities in tropical Australia (Whitehead 1985). Williams and Clarke (1983) have examined growth in juvenile and adult *Herklotsichthys quadrimaculatus* from Hawaii using the otolith increment technique. A. I. Robertson (MS in prep.) has used length-frequency data to estimate growth in juvenile *Herklotsichthys castelnaui* and *Sardinella albella* from mangrove nursery areas in tropical northeastern Australia. Dayaratne and Gjosaeter (1986) analyzed age structure of juveniles and adults in four species of *Sardinella* from Sri Lanka using daily growth increments on otoliths. Relatively few studies have measured larval age and growth in field situations; these parameters have not been reported for any tropical clupeid species.

In this paper, I examine daily increments in otoliths to determine some early life history parameters of a common clupeid of tropical northeastern Australia. *Herklotsichthys castelnaui* (*Harengula abbreviata* of many authors) is a coastal pelagic clupeid found along the eastern seaboard of Australia from Bloomfield (lat. 15°56′S) to Pambula (lat. 36°57′S; Whitehead 1985). Although little is known of the biology of *H. castelnaui*, it inhabits estuaries and inlets (Robertson and Duke 1987), spawning in summer (January–March) in the southern parts of its range (Blackburn 1941), but probably earlier in the year in more northern areas (Robertson, MS in prep.). There is no information available on larval biology.

The specific aims of this project were to

1) validate daily growth increments in the otoliths of larval *H. castelnaui*,
2) obtain estimates of daily growth for larvae in the field,
3) investigate relationships between otolith size, standard length, and age, and
4) determine the frequency distribution of larval birthdates during the spawning season.

METHODS

Collection of Larvae

Larvae were collected weekly from Breakwater Marina, Townsville, Australia (Fig. 1) during August to November 1987. The marina is some 5.2 hectares in area, with an average water depth of 5 m (mhw), and is connected to Cleveland Bay by a 30 m wide entrance. Water is flushed in and out of the marina during the normal tidal cycle. Cleveland Bay is shallow, approximately 25 km wide, and bounded by Magnetic Island on its eastern side (Fig. 1). Physical oceanographic parameters of the bay have been described by Walker (1981a, b).

Sampling was conducted at night using three fluorescent lamps sealed within a clear perspex tube and a 1 m × 250 μm mesh size plankton net. The lamps were switched on and the tube lowered into the water from a jetty to a depth of 1.5 m. The plankton net was then lowered approximately 3 m below the tube. The lamps were left on for 15 minutes, then the plankton net was hauled rapidly up over the perspex tube to the surface. This sequence was repeated 4 times during a sampling night at hourly intervals commencing at 20:00.

Almost all larvae were alive upon net retrieval and were transferred immediately into 98% ethanol for subsequent sorting and analysis. Handling specimens in this way minimized shrinkage (Theilacker 1980) and physical damage due to net capture (McGurk 1985).

Two species of clupeid larvae were collected from samples taken in the Breakwater Marina. These species were identified as *H. castelnaui* and *Escualosa thoracata* in a size series of specimens collected during the sampling period. Details of the number of *H. castelnaui* larvae collected and numbers analyzed for age and growth are given in Table 1.

TABLE 1.—Summary of sampling dates in 1987, number of *Herklotsichthys castelnaui* collected and numbers subsequently used for otolith examination.

Date	No. collected	No. analyzed
24 August	71	50
29 August	18	18
07 September	40	40
15 September	20	20
21 September	85	48
28 September	45	45
05 October	278	50
13 October	239	50
19 October	82	50
27 October	31	31

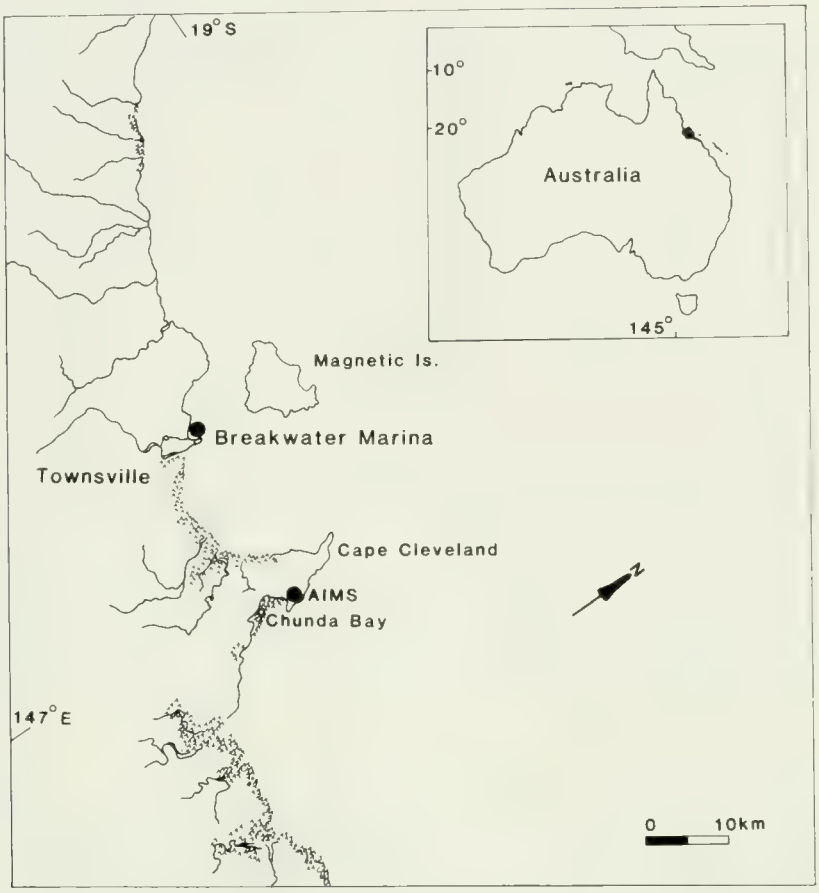

FIGURE 1.—Map of Australia showing position of Breakwater Marina, Townsville, where sampling was conducted from July to December 1987. Hatching indicates mangrove areas.

Otolith Preparation

Standard length of larvae (tip of snout to hypural crease or tip of notochord in preflexion larvae) was measured under a stereo dissecting microscope with an ocular micrometer. Measurement was made to the nearest micrometer unit (0.135 mm at 10× magnification). Specimens were placed in a drop of water on a microscope slide and otoliths were teased out with electrolytically sharpened tungsten needles. The larva was removed from the slide, and the otoliths air dried. To ensure dehydration, a drop of 98% ethanol was added to the otoliths and allowed to evaporate. Otoliths were then mounted in immersion oil for microscopic examination.

Individuals of *H. castelnaui* have three pairs of otoliths: sagittae, asterisci, and lapilli. Sagittae were the only otoliths found to be deposited during the first days of larval life, and subsequently only sagittae were considered in the analysis. Growth increments were visible in sagittae from larvae that ranged from 5 to 25 mm SL. These otoliths were viewed for counting under a compound microscope using polarized transmitted light. All counts were made at 1000× magnification. An Ikegami[3] high resolution video camera was mounted on the microscope, which was connected in turn to a video screen. Otolith increments were counted on the video screen as the increased contrast made rings easier to read. The system was interfaced with a Commodore Amiga personal computer for measurement of otolith radius and growth increment widths (Thorrold, MS in prep.). Otolith radius was measured from the center of the primordium to the outside

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

edge of the otolith, through the longest axis. Three counts were made of each sagitta, and the mean increment count from a pair of sagittae was used in the analysis. Otoliths were rejected if incremental counts within or between pairs of sagittae differed by more than two.

Validation of Ageing Technique

To determine if the increments observed in the otoliths of *H. castelnaui* were deposited daily, larvae collected from the marina were treated with tetracycline. Tetracycline is an antibiotic that is incorporated into calcium structures of fish during growth. This can be restricted to a single day's increment on the otolith (Tsukamoto 1985), and thus, the date of treatment can be accurately identified. This technique has become widely used in the validation of ageing techniques (e.g., Campana and Neilson 1982; Schmitt 1984; Kingsford and Milicich 1987).

Larvae were collected from Breakwater Marina on 14th of October 1987 and were transported to the laboratory at the Australian Institute of Marine Science (AIMS). The fish were kept in ambient photoperiod and temperature regimes for two days to allow time for acclimation. They were fed twice daily on wild zooplankton captured with a 15 μm mesh plankton net from Chunda Bay, adjacent to AIMS.

Ten fish were kept overnight in a 4 L tank treated with a 0.25 g/L tetracycline hydrochloride solution (Schmitt 1984). Four larvae died during exposure to the tetracycline. The remaining six larvae were returned to a 120 L tank and fed as before for 10 nights and 11 days before being sacrificed. Sagittae were dissected out of the remaining larvae and viewed under fluorescent UV and natural light with a compound microscope. Under fluorescent light an ocular marker was aligned with the fluorescent band in the otolith. The otolith was then examined under natural light, and the number of increments between the marker and the otolith margin counted. Both sagittae for each fish were analyzed, and three counts were made of each otolith.

Statistical Procedures

Laird-Gompertz and von Bertalanffy growth models were fitted to the length-at-age data. Both models have been shown to provide adequate fits to length-age data of 0+ fish in different situations (e.g., Ralston 1976; Laroche et al. 1982). Zweifel and Lasker (1976) presented a detailed discussion of the Laird-Gompertz function. The generalized equation of the model is

$$L_t = L_0 \exp[A_0/\alpha(1 - e^{-\alpha t})]$$

where L_t = length (mm) at age t; L_0 = length at $t = 0$; A_0 = specific growth rate at $t = 0$; and α = rate of exponential decay. Gallucci and Quinn's (1979) version of the von Bertalanffy equation was used, where the generalized equation of the model is

$$L_t = \omega/k \{1 - \exp[-k(t - t_0)]\}$$

where k = growth constant; L_∞ = maximum larval size obtained; $\omega = kL_\infty$; and t_0 = x-axis intercept.

The BMDP P3R[4] nonlinear least-squares regression program employing a modified Gauss-Newton algorithm was used to fit both models. A measure of goodness-of-fit was provided by calculating an r^2 value from residual and explained sums of squares derived from the least-squares regression. Goodness-of-fit can also be assessed by examination of standard errors and approximate 95% confidence intervals of parameter estimates.

Spawning frequency of *H. castelnaui* during the sampling period was estimated by ageing larvae and then back-calculating birthdates from the time of capture. Periodicity in spawning was analyzed using the SYSTAT SERIES[5] program, employing an autoregressive moving average (ARIMA) model (Box and Jenkins 1976). Autocorrelation of each value in a series with every other value will define relationships between all points in the series. A plot of partial autocorrelations will detect dependencies in the data, and identify the period of any dependency.

RESULTS

Otolith Morphology

Growth increments were clearly visible in sagittae of larval *H. castelnaui*. No marked changes in increment morphology was evident, although in some otoliths a narrowing and subsequent widening of increments occurred between increments 15 and 25 (Fig. 2). Counts of growth increments were obtained from 378 larvae ranging from 5.6 to 22.5

[4]BMDP 3R. 1983. BMDP statistical software. Univ. Calif. Press, Berkeley, CA 94720.
[5]SYSTAT SERIES. 1986. SYSTAT: The system for statistics. Evanston, IL 50201.

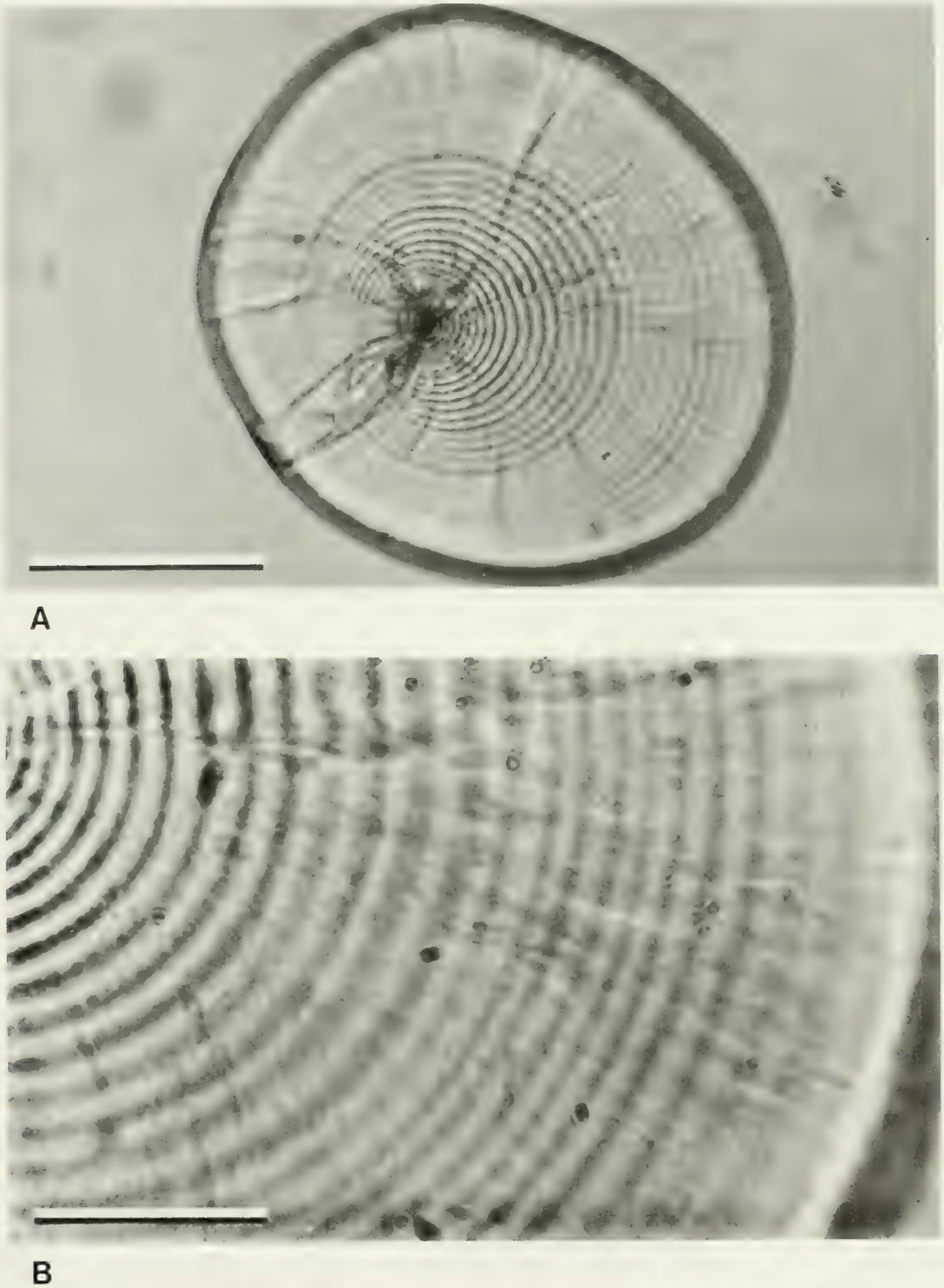

FIGURE 2.—*Herklotsichthys castelnaui*. Sagittae from larval herring showing daily growth increments of a 29 d old larva, 16.9 mm SL at (A) 250× (scale bar = 0.1 mm) and (B) 1000× (scale bar = 0.025 mm).

mm SL (see Figure 4), and from estimated ages of 3–53 days old. The increments were easily read in most otoliths; only 24 larvae were rejected due to either the error in reading precision being greater than 2 for the sagittae of a larva (10, 2.5%) or because otoliths could not be clearly read (14, 3.5%).

The plot of standard length (SL) against sagittae maximum radius (OD) revealed a logarithmic relationship (Fig. 3). Otolith diameter data were $\log_e$ transformed, and a regression equation fitted to the transformed data. This equation is described by

$$SL = 5.61.\log_e OD - 10.56$$

$$(n = 378;\ F = 2156;\ P < 0.0001;\ r^2 = 0.85).$$

Comparison of means from observed and predicted standard length values suggested that any bias caused by $\log_e$-transforming otolith diameter was neglible.

Validation of Ageing Technique

Increments were deposited daily in the sagittae of the six larval *H. castelnaui* kept under ambient conditions in the laboratory (Table 2). When viewed under natural light, a mean of 10 increments were visible from the fluorescent band to the margin of the sagittae. This corresponded to the number of nights that the fish were held after the tetracycline treatment.

Larval Age and Growth

It was assumed that the first otolith increment was laid down at hatching (see Discussion); therefore, the age of *H. castelnaui* larvae was estimated directly from the number of growth increments in the sagittae. Ages were thus minimum estimates for any given length. Descriptions of growth of larval *H. castelnaui* were based on age-at-length of 378

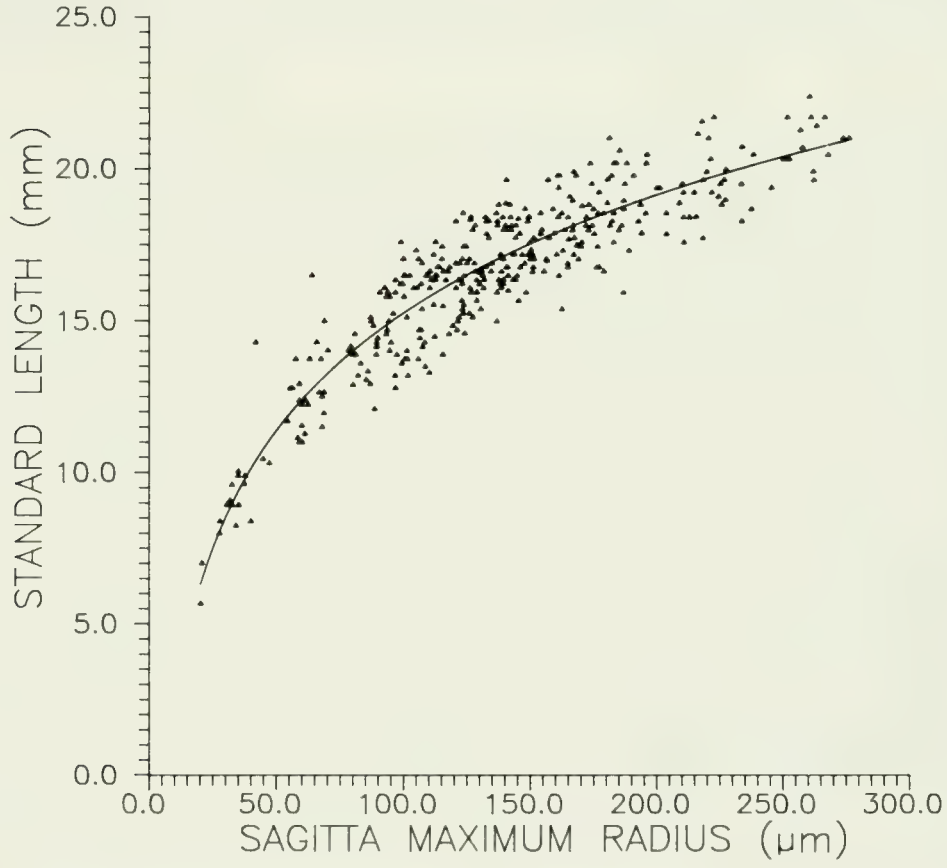

FIGURE 3.—Relationship between standard length and radius of sagittae for larval *Herklotsichthys castelnaui*, together with fitted logarithmic growth curve.

specimens, 5.6–22.5 mm SL. Laird-Gompertz and von Bertalanffy models yielded good and nearly identical fits to the data (r^2 = 0.74 for the Laird-Gompertz curve, r^2 = 0.75 for the von Bertalanffy curve); therefore, only the Laird-Gompertz growth curve is presented (Table 3; Fig. 4). This relationship does, however, appear to underestimate growth at ages less than 10. By contrast, the von Bertalanffy curve underestimated growth at ages greater than 38.

TABLE 2.—Validation of ageing using the tetracycline technique. Fish were preserved 11 days after treatment with tetracycline. Table shows standard length (SL), mean number of increments observed between the fluorescent band and the margin of both sagittae (± standard error), and the range of increment counts on each of the six fish.

Fish no.	SL	Mean ± SE	Range
1	20.6	9.5 ± 0.2	9–10
2	21.5	10 ± 0.5	9–11
3	21.0	10 ± 0	10
4	22.6	10.3 ± 0.2	10–11
5	22.6	10 ± 0.4	10–11
6	20.6	10 ± 0	10
Total		9.8 ± 0.1	9–11

TABLE 3.—Laird-Gompertz equation and estimated parameters describing growth of 378 *Herklotsichthys castelnaui* larvae. The growth model was fitted using nonlinear least-squares regression. STDERR = asymptotic standard error of parameter estimates; C.L. = approximate confidence intervals of parameter estimates.

Equation

$$L_t = 5.159 \exp[0.104/0.075\ (1 - e^{-0.075t})]$$

Parameters	STDERR	95% C.L.
L_0 = 5.159	0.348	L_1 = 4.474, L_2 = 5.843
A_0 = 0.104	0.011	L_1 = 0.082, L_2 = 0.125
α = 0.075	0.0054	L_1 = 0.064, L_2 = 0.086

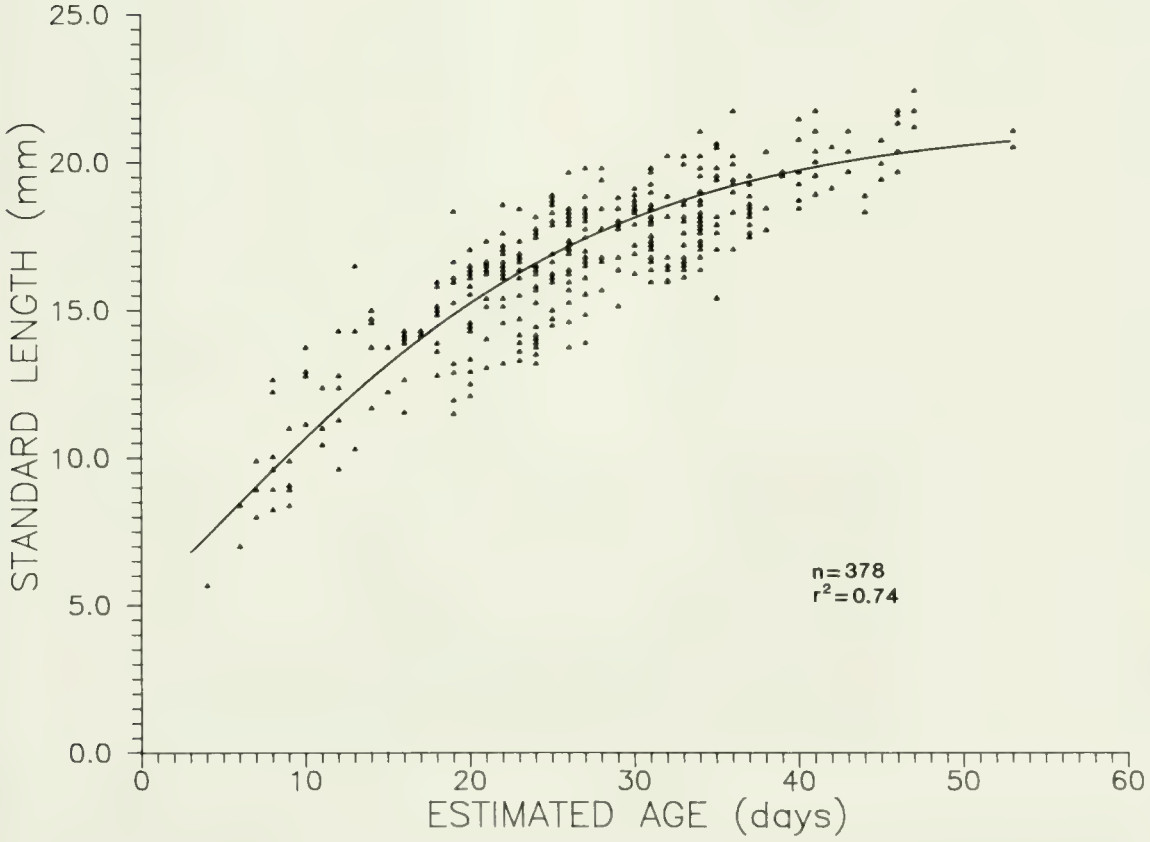

FIGURE 4.—Relationship between standard length and number of growth increments (increment number) on sagittae for larval *Herklotsichthys castelnaui*, together with fitted Laird-Gompertz growth curve.

Estimates of specific and absolute growth rates (Table 4) were calculated from length-at-age (L_t) for various ages as predicted by the Laird-Gompertz equation

$$L_t = 5.26 \exp[0.104/0.075\ (1 - e^{-0.075t})].$$

Specific growth rate declined from 7.4% to 1.1% per day SL at 30 days after hatching, before levelling off at around 0.5% per day SL over the latter half of larval life. Absolute growth showed a similar pattern, with a rapid decline from a maximum value of 0.57 mm/d at day 5 to a value of approximately 0.1 mm/d approaching metamorphosis, 40–50 days after hatching.

Spawning occurred over three months (mid-July to mid-October), peaking around the first week in September (Fig. 5). There are indications of lunar periodicity within those months; spawning peaks were separated by approximately two weeks, apparently associated with first and third quarter moon phases. Time series analysis also indicated a 14 d periodicity in spawning peaks. Autocorrelation coefficients larger than two standard errors of the mean autocorrelation coefficient are considered significant (fn. 5). Coefficients greater than this value (0.29) occurred on day 0 (0.62) and day 14 (0.39), indicating the existence of a periodicity in the data of 14 days.

TABLE 4.—Growth rates of *Herklotsichthys castelnaui* larvae predicted from the Laird-Gompertz growth equation at various times after hatching.

Age (days)	Specific growth rate (%/d SL)	Absolute growth rate (mm/d)
4–5	7.4	0.57
9–10	5.1	0.53
14–15	3.5	0.45
19–20	2.4	0.36
24–25	1.7	0.27
30–31	1.1	0.20
34–35	0.8	0.15
40–41	0.5	0.10
44–45	0.4	0.08

DISCUSSION

Clear growth increments consisting of alternating light and dark bands were visible in all three pairs of otoliths in *Herklotsichthys castelnaui*. Asterisci and lapilli were formed, however, some time after the sagittae. This suggested that the number of

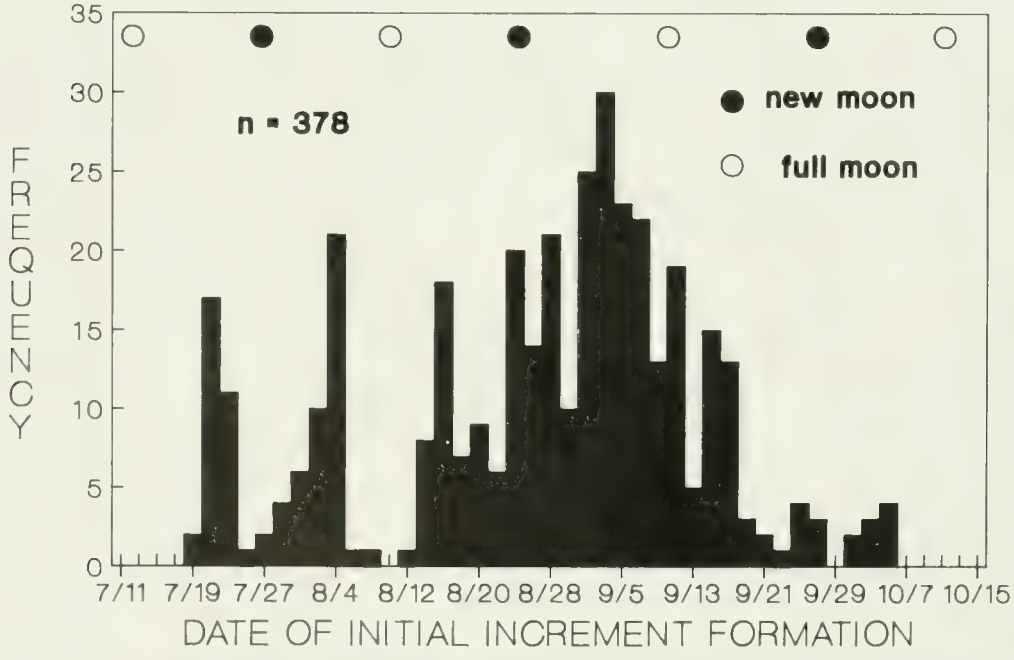

FIGURE 5.—Spawning periodicity of *Herklotsichthys castelnaui* based on back-calculated dates of initial increment formation. Frequency values are 2 d class means, two increments being the maximum accepted error in increment counts.

growth increments on the sagitta provided the closest estimate of age in larval *H. castelnaui*.

Age at initial increment deposition was not determined in this study. Initial growth increments have been shown to be deposited prior to egg hatching, at hatching, just after hatching, and at onset of exogenous feeding (Brothers et al. 1976; McGurk 1984; Kingsford and Milicich 1987). All temperate clupeids studied have initiated ring formation at yolk-sac absorption (Geffen 1982; Lough et al. 1982; McGurk 1984; Re 1984) from 3 to 5 days after hatching. Although no work has been published on otolith formation in tropical clupeids, a comparatively high water temperature, and hence a rapid developmental rate, suggests that endogenous reserves would be quickly exhausted (Houde 1974). It was thus assumed here that the first otolith increment is laid down at hatching, and otolith counts were assumed to be a direct measure of age. Violation of this assumption will have led to biased estimates of L_0, the size at hatching, and A_0, the specific growth rate at hatching, in the Laird-Gompertz model. The magnitude of absolute and specific growth rates remain valid. The age at which the growth rates were calculated will, however, have a systematic error corresponding to the time from hatching to initial increment formation.

Standard length increased as a logarithmic function of otolith radius. Linear (e.g., Rice et al. 1985), logarithmic (Nishimura and Yamada 1984; Tsuji and Aoyama 1982), and some combination of the two functions (Jenkins 1987) have been reported in the literature. A close correlation between standard length and otolith growth at a daily level implies that the width of any growth increment is a measure of instantaneous growth (Campana and Neilson 1985). The smoothly monotonic relationship between standard length and otolith radius presented here suggests that it may be valid to reconstruct individual growth histories by examination of growth increment spacings in sagittae of *H. castelnaui*.

Both Laird-Gompertz and von Bertalanffy growth curves adequately fitted the length-at-age data. The growth trajectory of larval *H. castelnaui* indicates that growth is rapid for the first two to three weeks, but slows after this period. Growth may become asymptotic after this point, as predicted by the single cycle Laird-Gompertz model, or alternatively, enter a new growth stanza during juvenile life, as has been reported for *Herklotsichthys quadrimaculatus* (Williams and Clarke 1983).

Data presented here for larval *H. castelnaui* affords good comparison with some temperate clupeid species, where growth rates have also been elucidated using the otolith increment technique. Initial growth rates of 0.5–0.6 mm/d in *H. castelnaui* are as high as any recorded for clupeid larvae in the field. Similar growth estimates have been reported off South West Africa, where *Sardinops ocellatus* larvae grow linearly at rates of approximately 0.7 mm/d (Thomas 1986). Growth estimates of 0.2–0.4 mm/d after this initial burst are closer to those presented for *Clupea harengus* from the northern Atlantic (Townsend and Graham 1981; Lough et al. 1982; Henderson et al. 1984). Growth rates of larval *H. castelnaui* may reflect higher ambient water temperatures, as both *S. ocellatus* and *C. harengus* have a higher L_∞ and hence higher predicted growth rates (Ricker 1975).

Spawning periodicity in *H. castelnaui* was apparently correlated with the quarter moon phases. Lunar-synchronized spawning has been reported in salmoniform, atheriniform, tetraodontiform, and perciform fishes (Taylor 1984). Most fish species with lunar-spawning rhythms spawn on or around the new or full moon (e.g., Lobel 1978; Middaugh et al. 1984), although spawning in French grunts, *Haemulon flavolineatum*, also appears to be coupled with quarter moons (MacFarland et al. 1985). It should be noted that results presented here may be subject to some systematic error in ageing. If, for example, initial increment formation occurs some time after hatching, then birth dates will have been consistently underestimated. MacFarland et al. (1985) hypothesized that currents favorable for settlement may account for fertilization and recruitment events peaking on the quarter moon. My results suggest that spawning occurs with some semilunar periodicity, but the time of initial increment formation needs to be determined before relating spawning events to moon phases and possible tidal influences on egg and larval distributions.

The most significant advantage of using otolith ageing techniques is the ability to produce individual rather than population statistics. Although it has been possible to fit a growth equation to the length-age data presented here, there is also an amount of variability surrounding the curve. This variability may, at least in part, be a sampling artifact caused by methodological problems. Inaccurate age determinations may be caused by nondaily deposition of rings under some conditions (e.g., Geffen 1982), or failure to detect all rings within an otolith due to the resolution problems of light microscopy (Campana et al. 1987). Conversely, if the data are accurate, variable growth rates on small spatial (tens of meters) and temporal (days) scales are detectable by otolith analysis. It is often tacitly assumed in lar-

val studies that a fast growth rate will be reflected in lower mortality rates, although the implications of fast or slow growth to subsequent survivorship have yet to be addressed. Otolith analysis emphasizing individual rather than population growth parameters may provide a tool for approaching such questions in field situations.

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ENERGETIC AND BEHAVIORAL EFFECTS OF NET ENTANGLEMENT ON JUVENILE NORTHERN FUR SEALS, *CALLORHINUS URSINUS*

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ABSTRACT

The energetic costs and behavioral changes associated with net entanglement were studied in three captive juvenile male northern fur seals, *Callorhinus ursinus*. Rates of energy expenditure were highly dependent upon swim velocity and size of the net fragment. At a speed of 1.1 m/s, northern fur seals expended a mean (±SD) of 6.5 (±0.7) W/kg before entanglement, 9.7 (±3.8) W/kg when entangled in 100 g nets, and 13.8 W/kg with 200 g nets. These results showed that a free-ranging animal entangled in a net fragment of 200 g or larger will experience considerable difficulty swimming.

The northern fur seals' average daily metabolic rates (ADMR) were measured with doubly labeled water over 6 day periods before and during entanglement in 225 g net fragments. Concurrent behavioral observations revealed a 75% reduction in time spent swimming and a 138% increase in time spent resting due to entanglement. Nevertheless, the northern fur seals' mean ADMR rose from 8.0 (±0.4) W/kg to 9.3 (±1.9) W/kg. While this increase was primarily due to one animal's performance, it suggests that entanglement may also elevate the costs of resting and grooming.

At 17 months of age, the northern fur seals had averaged head diameters (±SD) of 14.7 (±0.2) cm, making them most susceptible to entanglement in nets with stretched mesh sizes of 23 cm or more. Observations showed that these juvenile fur seals were naturally inquisitive and rapidly became entangled upon their first encounter with a floating net. Subsequent entanglements depended more upon each animal's behavior than upon net fragment size. Captive animals were unable to free themselves from the entangling fragments.

Since the mid-1950's, the Pribilof Island population of northern fur seals, *Callorhinus ursinus*, has undergone several declines. The initial reduction in population size can be attributed to a harvest of adult females, conducted from 1957 through 1968 (York and Hartley 1981). However, from 1974 until 1981, the number of pups born each year continued to decline (Fowler 1985; York and Kozloff 1987). As a result, the present northern fur seal population numbers 800,000 animals, down from an estimated 1.2 million in 1976.

In the mid-1960's, the percentage of young male northern fur seals found entangled in synthetic trawl net fragments and other marine debris began to rise, reaching a peak of about 0.7% in 1975 (Fowler 1987). Since 1976, the entanglement rate has remained roughly stable at 0.4% of the subadult male population. The northern fur seal population declines, concurrent with the rising entanglement rate, have led some authors to speculate that entanglement may be one contributing factor (Fowler 1985, 1987). Using available data on entanglement rates, net size distribution, and assumed mortality rates, Fowler (1982) derived and demonstrated a model that entanglement induced mortality could account for the current population trends. Although based on several unverified assumptions, it nonetheless points to the potential seriousness of net entanglement.

Several lines of indirect evidence suggest that entanglement related mortality has its greatest impact on younger age classes (less than 2–3 years old). Since 1965, the at-sea survival rate of 0–2 yr old northern fur seals has declined relative to the survival rate of nursing pups on land (Fowler 1985). Prior to 1965, these parameters were positively correlated. Furthermore, this decline in the expected survival rate is correlated with the increased incidence of observed entanglements (Fowler 1985). Working with captive animals, Yoshida and Baba (1985) have also demonstrated that younger animals entangle themselves more frequently than older ones. The impact of entanglement would be more severe on these smaller animals; because of their size, smaller animals will suffer relatively higher drag and greater power requirements during swim-

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ming than would larger animals entangled in a similar-sized fragment (Feldkamp 1985).

Many questions remain unanswered concerning the impact of marine debris on the demographics of northern fur seals. While it is virtually impossible to directly measure mortality arising from entanglement in different age and sex classes, measurements can be made of the behavioral changes and energetic costs associated with entanglement, the susceptibility of different age classes to entanglement, and the effects of net size on these parameters. In this study we examine the energetic and behavioral costs associated with entanglement. The swimming metabolic rate of three juvenile male northern fur seals entangled in various-sized nets was measured. Changes in behavior and average daily energy expenditure during extended periods of entanglement were quantified. The northern fur seals' responses to floating debris, the likelihood of entanglement, and their ability to free themselves after entanglement were also examined to provide a better understanding of the biological consequences of net entanglement in these animals.

MATERIALS AND METHODS

Three newly weaned male northern fur seal pups (age = 4 months, based on estimated birth date of July 1; Gentry 1981) were captured on St. Paul Island, AK in November 1985. They were transported to the Marine Laboratory, University of California at Santa Cruz and placed in a large holding tank supplied with filtered seawater. Twice per day, the animals were fed a ration of herring supplemented with vitamins.

These three northern fur seal pups were weighed weekly. Measurements of standard length (nose to tip of tail) and of girth around the head (at ears), neck, and shoulder region were made at several month intervals. Girths were converted to diameters by assuming a circular circumference.

Net fragments used in this study were all cut from polypropylene trawl nets found on St. Paul Island, AK. Each fragment had a stretched mesh size of 23 cm (9 in). The twine had a diameter of 3 mm (⅛ in).

Swimming Energetics

The energetic cost of swimming, before and during entanglement, was measured by placing the northern fur seals in a water flume constructed inside of a circular tank, 7.6 m in diameter and 2.7 m deep. A wooden ring (4.9 m in diameter and 1.2 m in height) was placed in the tank, forming a 1.3 m wide channel between it and the tank wall. A water current was generated inside this channel with two pumps. The first, a 15 hp pump, was submerged to a depth of 48 cm and produced a flow of 0.75 m/s. The second, a 10 hp nonsubmersible pump, was located above the tank with its intake and outlet hoses fixed in the channel; this pump could generate flows of 0.6 m/s. Run simultaneously, the two pumps created flows of 1.1 m/s.

The fur seals swam inside of a metabolic test section (2.2 m in length, 1.1 m wide, 0.9 m deep) constructed in the channel. The walls of the tank and inner ring formed its sides. Front and back ends were framed with wood and covered with 8 cm × 13 cm mesh wire screen. A sheet of plywood covered the top. A plastic dome (0.9 m × 0.6 m × 0.3 m) was set into this plywood and served as an open circuit metabolic chamber. Animals in the test section could only surface to breathe inside of the dome.

To minimize turbulence, the test section was located approximately 7.5 m away from the outflow of the pumps, along the tank's circumference. Water velocity was measured with a General Oceanics Model 2035 MKIII[3] flow meter, accurate to ±3%. All flow measurements were made in the test section, 50 cm from the floor and 90 cm from the front screen.

Air was drawn through the metabolic dome at a rate of 20 L/min. Oxygen content of the air was measured with an Ametek oxygen analyzer calibrated using the methods of Fedak et al. (1981). A computer monitored the analyzer's output each second and produced a 1 min average of the percent O_2 concentration. Oxygen consumption ($\dot{V}O_2$) was calculated using equation 11 of Fedak et al. (1981). Every 10 minutes, these minute readings were averaged to provide single data points at each swimming speed. All values were corrected to STPD, and $\dot{V}O_2$ (in mL $O_2 \cdot min^{-1} \cdot kg^{-1}$) was converted to W/kg by assuming a caloric equivalent of 20.1 J/mL O_2 (Bartholomew 1977).

Prior to the actual measurements, the three northern fur seals were trained for several weeks to swim in the flume. Training was considered complete when consistent values for $\dot{V}O_2$ were obtained at each speed. During experiments, 12 h fasted animals were placed in the flume and allowed to rest, groom, or swim at their own speed for approximately 15 minutes while $\dot{V}O_2$ was monitored. The first water pump was then turned on and water velocity maintained at 0.75 m/s. Ten minutes were allowed for

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

animals to reach a steady state and then $\dot{V}O_2$ measurements were made for 20–30 minutes. The second pump was then activated, creating a water speed of 1.1 m/s, and $\dot{V}O_2$ was monitored as described above. Only those trials where steady swimming occurred were used in the final calculations of metabolism. Experiments that reversed the order of swimming speeds revealed no differences in $\dot{V}O_2$ that could be attributed to the effects of ordering.

Each fur seal was run once per day over a 2 wk period until baseline values were established. Fur seals were then entangled in small net fragments and the measurements were repeated. All three animals were run daily, and trials with one net size were completed before beginning the next size. For each net size, experimental trials lasted approximately 2 weeks.

Nets were attached by placing the fur seal's head through a wire ring, 15 cm in diameter, sewn into the center of each fragment. Three sizes of net were used in the following order: 61, 100, and 200 g with dimensions of 4 × 4 meshes (0.6 m × 0.6 m), 7 × 4 meshes (1.2 m × 0.6 m), and 7 × 7 meshes (1.2 m × 1.2 m), respectively. Nets were folded over once (100 g), or twice (200 g) to prevent fouling of the foreflippers, and were removed after each session.

Experiments were run both in the winter and spring. Winter experiments were conducted at a single flume speed of 0.75 m/s using 61 g and 100 g nets. During the spring, 100 g and 200 g nets were used at flume speeds of 0.75 m/s and 1.1 m/s. At the completion of the spring trials, baseline values were again established through daily runs conducted without nets.

Behavioral and Energetic Changes Associated with Entanglement

In this study, the effect of entanglement on the northern fur seals' behavior and average daily metabolic rate (ADMR) was measured. The fur seals were 14 months old and weighed an average (±SD) of 19.1 (±1.0) kg. They were kept in a circular holding tank, 7.6 m in diameter and 1 m deep with no haul-out provided.

Two experiments were undertaken. First, free-swimming fur seals were monitored over a 6 d period. They were then entangled in 225 g net fragments and the measurements were taken for another 6 days. A nylon dog collar, sewn into the middle of each fragment, was used to fasten the net around the animal's neck.

The ADMR of each fur seal was determined before and during entanglement using isotopic tracers (Nagy 1980; Schoeller and van Santen 1982; Costa and Gentry 1986). Prior to each experiment, blood samples were taken, and then the animals were injected interperitoneally with 5.5 mL of 0.66 mCi tritium (HTO) per mL and 2.5 g of $H_2{}^{18}O$ at 95 atoms percent. After equilibration (3 hours), a 10 cc blood sample was taken from a flipper vein and the animal was released into the tank. After the 6 d measurement period, fur seals were removed from the holding tank, and final blood samples were taken.

Tritium specific-activity in water that was vaccum distilled from blood samples was determined by liquid scintillation spectrometry. Oxygen-18 levels were measured by isotope mass ratio spectrometry in a commercial laboratory (Global Geochemistry, Canoga Park, CA). Rates of CO_2 production ($\dot{V}CO_2$) were calculated using equation 2 in Nagy (1980), and water flux rates determined using equation 4 in Nagy and Costa (1980). We assumed an RQ of 0.80 to calculate energy consumption.

The northern fur seals' behavior over the course of each study period was quantified using a discontinuous time sampling method (Tyler 1979). Every hour, from 0800 to 2000, the fur seals were observed for 10 minutes. At exactly 1 min intervals during this period, the behavior displayed by each fur seal was noted. Behaviors were broken into four categories: swimming, grooming, resting, and other activities. Animals were considered to be swimming when they were actively stroking or gliding between strokes. Grooming was defined as scratching, rubbing the fur, or shaking the head. Animals at rest were lying quietly, often holding their flippers out of the water. Activities such as rolling, nuzzling one another, or other slow movements were placed in the "other" category.

Entanglement Observations

The reactions of northern fur seals to the presence of floating nets, their ability to free themselves after entanglement, and the likelihood of entanglement in net fragments of various sizes were investigated. Two fur seals were placed in a 7.6 m diameter holding tank, 1 m deep, along with floating net fragments of various sizes, and were denied access to haul-out areas during this time. The time from net presentation to entanglement was recorded and correlated with fragment size. Once entangled, nets were left on for periods ranging from several hours to several days.

RESULTS

Measurements of the northern fur seals' length, mass, and body diameters as a function of age are presented in Table 1.

TABLE 1.—Age[1], weight, length, and body diameters of the three northern fur seals used in this study. Means (±SD) are given.

Age (mo)	Mass (kg)	Length (cm)	Diameter (cm) at ears	neck	shoulders
4	14.4 (2.02)	87.7 (1.56)	13.5 (0.15)	14.9 (0.40)	21.1 (1.02)
12	19.6 (1.21)	102.3 (1.16)	14.3 (0.00)	15.8 (0.46)	21.4 (1.25)
17	21.3 (0.70)	107.7 (2.08)	14.7 (0.23)	16.8 (0.51)	22.9 (0.30)

[1]Age based on estimated birth date of July 1

Energetic Measurements

During the winter swimming trials, mean water temperature (±SD) was 14.9 (±0.2) °C. Mean body mass of the three northern fur seals was 14.1 (±0.6) kg. At zero water flow, fur seals expended a mean of 6.95 (±1.02) W/kg; at 0.75 m/s it was slightly, though not significantly, lower and averaged 6.89 (±0.45) W/kg (Table 2). The greater metabolic rate at zero flow was due to uncontrolled activity (swimming and grooming) inside the chamber. At 0.75 m/s the animals swam steadily and did not groom.

At zero water flow, the presence of a net also slightly increased each fur seal's metabolic rate (Fig. 1). Although there was no evidence of any behavioral change, the net may have caused slight stress and led to an elevated O_2 consumption. Additionally, there may have been a loss of air from the pelage in the region of the net allowing the infiltration of cold water. This rise was noted both in the winter and spring experiments (Table 2).

At the relatively slow speed of 0.75 m/s, small net fragments did not significantly elevate mean metabolic rates (Fig. 1b). In fact, metabolism was 3.5% lower with a 61 g net at 0.75 m/s than at zero flow (Table 2). While a slight elevation did occur with the 100 g net at 0.75 m/s, this was not significantly greater than at zero flow with a 100 g net or than at 0.75 m/s with no net (Fig. 1b).

During the spring experiments, water temperature had increased to a mean of 16.6 (±0.5) °C, and the fur seals had increased in weight to 16.4 (±0.5) kg (Table 2). As a result, each animal's routine energy consumption, determined at zero flow and without a net, had declined to a mean of 5.22 (±0.21) W/kg. This decline was also evident when the results of the winter and spring experiments at 0.75 m/s and with 100 g net fragments were compared (Table 2).

As noted during the winter trials, animals with 100 g nets did not expend greater amounts of energy at 0.75 m/s than during unentangled swimming at this speed. At 1.1 m/s, however, a 100 g net caused a significant 40% increase in metabolic rate (*t*-test; $P < 0.05$) (Fig. 1c). The 200 g fragments caused significant metabolic increases at both flume speeds. When entangled in a fragment of this size, fur seals expended 66% more energy at 0.75 m/s than at zero flow speed. At 1.1 m/s, mean metabolic rate was elevated 2.1 times that measured for unentangled

TABLE 2.—Mean (±SD) rate of energy utilization (W/kg) for the three northern fur seals during the winter and spring swimming experiments. Means were determined by combining data from all animals. The sample size for each animal (FS1, FS2, FS3) is given in parentheses (n_1, n_2, and n_3, respectively). Body mass and water temperature averaged 14.1 (±0.55) and 14.9 (±0.2) °C in the winter, and 16.4 (±0.5) kg and 16.6 (±0.5) °C in the spring.

	Winter			Spring		
		Net size			Net size	
Flume speed	No net	61 g	100 g	No net	100 g	200 g
0 m/s	6.95	8.26	7.78	5.22	6.10	5.90
±	1.02	0.91	0.71	0.21	0.85	0.78
(n_1, n_2, n_3)	(8, 7, 6)	(6, 5, 5)	(5, 6, 5)	(6, 6, 5)	(4, 4, 4)	(6, 7, 6)
0.75 m/s	6.89	7.98	8.40	5.21	6.89	8.63
±	0.45	1.87	1.65	0.32	0.42	1.52
(n_1, n_2, n_3)	(8, 7, 6)	(5, 6, 5)	(6, 5, 5)	(5, 5, 5)	(4, 4, 4)	(6, 7, 6)
1.1 m/s				6.54	9.68	13.83
±				0.72	3.79	1.27
(n_1, n_2, n_3)				(5, 5, 5)	(6, 4, 4)	(6, 7, 6)

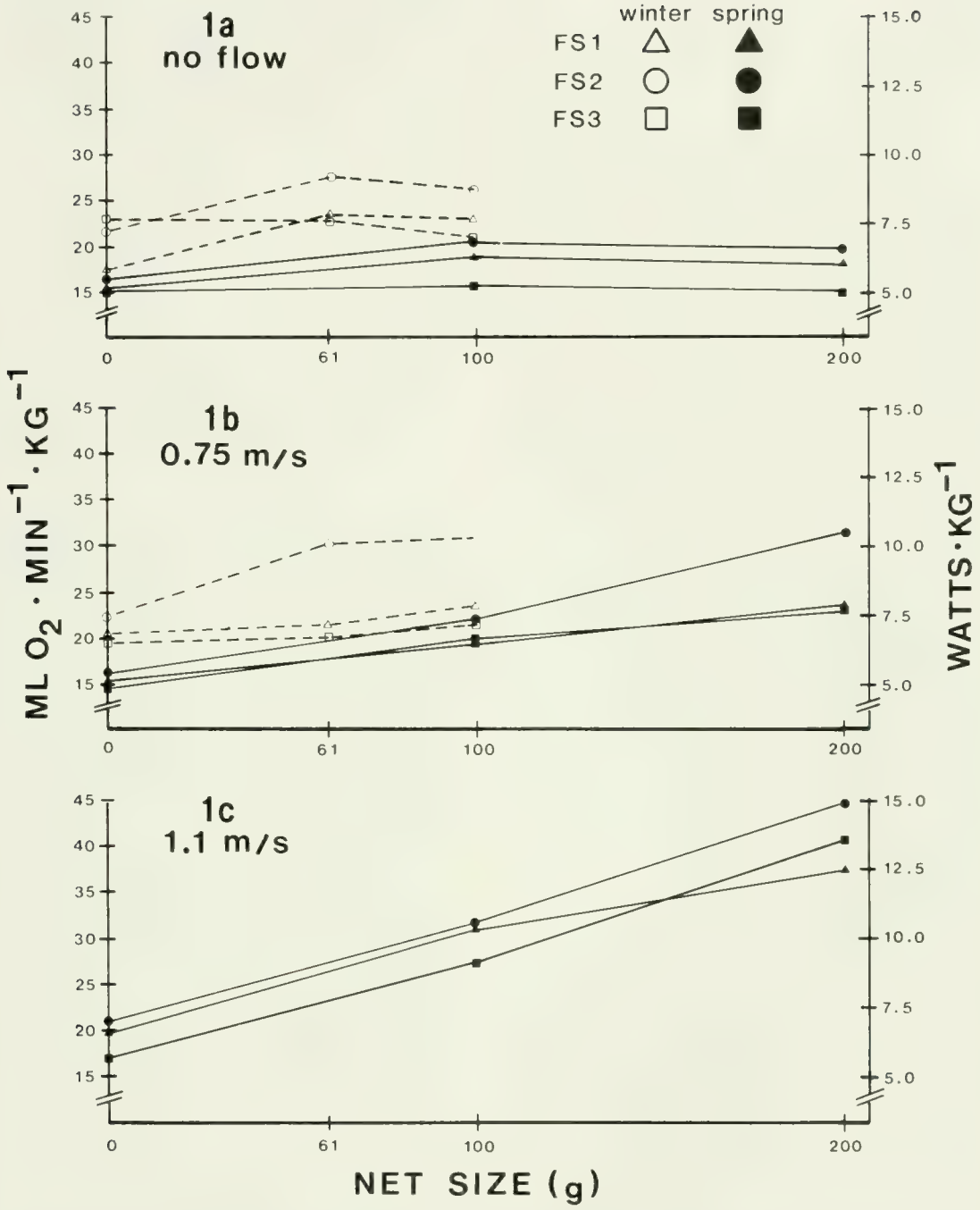

FIGURE 1.—$\dot{V}O_2$ (mL O_2 · min^{-1} · kg^{-1}) and energy expenditure (W/kg) of three northern fur seals plotted as a function of net fragment size. a) Measurements at zero flow speed, b) measurements at 0.75 m/s, and c) measurements at 1.1 m/s. Open symbols and dashed lines are measurements conducted during the winter; solid symbols and lines are from the spring.

swimming at this speed, and 2.7 times that measured at zero flow (Fig. 1c). All animals with 200 g nets struggled against the flow at 1.1 m/s.

Behavioral and Energetic Changes Associated with Entanglement

Before entanglement, swimming was the predominate behavior of the northern fur seals (Table 3). Grooming was the next most frequent activity, while resting accounted for 18% of the total activity. After entanglement in a 225 g fragment, the fur seals' behavior was substantially altered. Time spent swimming declined by roughly 75% from control measurements, while the percent time spent resting increased by a factor of 2.4. Time spent grooming, however, was not significantly altered; fur seals continued to spend approximately 1/3 of their daylight hours engaged in this activity (Table 3).

TABLE 3.—Percentage of time spent by three northern fur seals at swimming, resting, grooming, or in other activities over 6 d intervals before and during entanglement in a 225 g net.

	Before entanglement				During entanglement			
Animal	Swim	Rest	Groom	Other	Swim	Rest	Groom	Other
	% time				% time			
FS1	36.2	23.4	33.4	7.0	6.1	55.0	28.4	10.5
FS2	49.2	15.0	29.4	6.4	21.0	36.1	38.4	4.5
FS3	44.3	15.7	28.5	11.5	5.2	37.6	30.6	26.6
Mean	43.3	18.0	30.4	8.3	10.8	42.9	32.5	13.8
(± SD)	(6.6)	(4.7)	(2.6)	(2.8)	(8.9)	(10.5)	(5.3)	(11.4)

The nature of the resting and grooming behaviors of fur seals appeared to change as a result of entanglement. Unentangled fur seals typically rested quietly on the surface in a "jug-handle" position with one foreflipper and both rear flippers held out of the water. Entangled fur seals most often rested with their ventral surfaces down and both fore- and rear flippers submerged. In this position, they had to lift their heads to breathe. Resting was also not completely quiet. Unlike before, fur seals changed positions frequently and were always alert in the presence of observers.

When grooming, fur seals spent more time violently shaking their heads and scratching at the net with both their rear and foreflippers than before entanglement. Grooming was less vigorous in the absence of a net. More time was spent slowly rolling around in the water, or passively moving about (Table 3).

The rate of energy expenditure during entanglement was slightly greater than in the control experiment, although this difference was not significant. While mean ADMR increased by 16% after entanglement (Table 4), this increase was primarily due to one animal (FS2). FS2 swam more than either of the other two animals both before and during entanglement (Table 3), and this undoubtedly led to a higher ADMR.

No consistent trend was observed for FS1 and FS3 with respect to altered energetic expenditures associated with entanglement. FS1's metabolic rate increased 1 W/kg above the control measurement. FS3 showed a decrease of roughly the same amount (Table 4). FS1 exhibited an increased ADMR even though it spent less time swimming and grooming during the entanglement period. While FS3 showed similar behavioral trends, its ADMR decreased during entanglement.

TABLE 4.—CO_2 Production ($\dot{V}CO_2$ in L $CO_2 \cdot h^{-1} \cdot kg^{-1}$) and rate of three northern fur seals' energy expenditure[1] (W/kg) determined by the doubly labeled water method. Measurements were made over 6 d intervals before and during entanglement in a 225 g net.

	Before			During			%
Animal	Mass	$\dot{V}CO_2$	W/kg	Mass	$\dot{V}CO_2$	W/kg	change
FS1	19.9	1.12	7.79	20.5	1.28	8.90	+14
FS2	17.8	1.12	7.81	18.6	1.63	11.34	+45
FS3	18.9	1.22	8.51	18.9	1.08	7.50	−12
Mean	18.7	1.15	8.04	19.3	1.33	9.25	
(± SD)	(1.05)	(0.06)	(0.41)	(1.02)	(0.28)	(1.94)	

[1]Calculated using an RQ of 0.80.

Entanglement Observations

Individual variations in behavior were the most important factors influencing whether entanglement occurred (Table 5). For example, FS1 became entangled 1 hour and 45 minutes after it was first presented with a 6 × 4 mesh net (0.9 m × 0.6 m). From presentation to entanglement, the net was the focus of the animal's attention. FS1 bit and pulled at it, laid beneath it, and often rested on top of it. Once entangled, FS1 became quite agitated and swam around vigorously while violently shaking its head. The holding tank was drained after 1 hour and the net was removed from its neck. Another net (4 × 4 meshes; 0.6 m × 0.6 m) was then introduced into the holding tank and FS1 ignored it completely throughout the rest of the day. By the following morning, FS1 had become entangled again. This net was left on the animal for 2 days. At no time did it appear that FS1 could free itself, and the net was subsequently removed. Another net was then

introduced, and this time it was completely ignored. After 8 hours, the net was removed from the tank.

In contrast to FS1's apparent increased wariness to floating nets after its first entanglement, FS3 became entangled almost immediately on every net presentation (Table 5). Upon encountering the first net, FS3 played with it constantly, exhibiting similar behaviors as shown by FS1. Within 20 minutes FS3 had entangled itself. This net was left on for 2 days without the animal freeing itself and was then removed by hand.

Approximately one week later, FS3 was presented with a second, smaller net, and it quickly became entangled. Rather than remove this net, another small net was introduced into the tank. Within 30 minutes, FS3 became entangled in this as well. The tank was subsequently drained and both nets were removed. The tank was then refilled and a net immediately placed in the water. Within 10 minutes the animal became entangled. Two additional nets were then placed in the water. Within 1 hour, FS3 had become entangled in these as well. All three nets were then removed from the animal's neck.

TABLE 5.—Entanglement observations of two captive northern fur seals held in a 7.6 m diameter, 1 m deep circular holding tank. The net used had a 23 cm stretched mesh size.

Animal	Date	Net size (meshes)	Time to entanglement
FS1	2/15	6 × 4	1 h 45 min[1]
	2/15	4 × 4	<20 h[2]
	2/17	6 × 4	No entanglement in 8 h
	2/20	6 × 4	2 h 15 min
	2/20	6 × 4	<6 h
FS3	1/29	6 × 4	23 min[1]
	2/11	4 × 4	14 min[3]
	2/11	4 × 4	28 min
	2/11	6 × 4	8 min[3]
	2/11	4 × 4	37 min (1)[3]
		(two nets)	30 min (2)
	2/12	6 × 4	36 min

[1]First presentation of a net.
[2]Net left floating in water over night.
[3]Net left on animal when next one was introduced into the tank.

From these and from subsequent observations (Table 5), it is unclear whether net fragment size influences the probability of entanglement. FS3 became entangled almost immediately following every net presentation, regardless of the net's size. FS1, however, seemed to be wary of nets following its first entanglement. This wariness appeared to subside after several days without encountering a net.

Video recordings made of FS3 documented the behaviors preceding and following an entanglement. While playing with the net, FS3 approached from below and began to inspect it. After several seconds, FS3 pushed its nose up through a mesh opening in an apparent attempt to breathe. Immediately upon sensing the net around its muzzle, FS3 attempted to free itself by quickly shaking its head from side to side. This served to pull the net further down its head and, within several seconds, meshes were tightly wrapped around the animal's neck. During this time, and immediately following, FS3 became extremely agitated. It continued its quick and violent headshaking, but also began to swim rapidly around the tank, porpoising frequently. This action undoubtedly caused the net to be pulled even further down its neck. After approximately 2 minutes, swimming slowed, but FS3 continued to stop and shake its head violently. Approximately 5 minutes later, FS3 had several meshes looped over its head and neck.

FS3's eating ability was not impaired by the net, and so it was left on for 2 days. There was never any indication that the animal would be able to free itself and the net was finally removed. Although the net was so tightly wrapped around the animal's neck that it had to be cut off, there was no evidence of abrasions or lacerations.

DISCUSSION

In a recent review, Fowler (1987) suggested that younger northern fur seals are more prone to entanglement related mortality than are older animals. Results from the present study help to shed light on possible reasons for these apparent age related discrepancies. Small physical size and the inquisitive nature of juvenile animals are likely to be the two important factors leading to a higher mortality from entanglement. Naive animals may become entangled with greater frequency than older, perhaps less inquisitive animals, and smaller animals have the potential to become entangled in a greater range of mesh sizes. Moreover, once entangled, relative swimming costs will be higher for smaller animals (Feldkamp 1985).

The majority of nets found on two Alaskan islands (St. George and Amchitka) had stretched mesh sizes of 20 cm or less, with a mode of 10–15 cm (Fowler 1987). If this is representative of material adrift at sea, then most fragments have a small mesh size. It seems reasonable to conclude, therefore, that relative to larger animals, a greater number of fragments exist that are potentially hazardous to smaller

animals. Young fur seals are most often found in trawl net fragments having a stretched mesh size of 20 cm or more, with 23 cm mesh observed most frequently (Scordino 1985). The diameter of a 23 cm mesh is 14.6 cm, almost exactly the average head diameter of the captive 17 mo old northern fur seals (Table 1). Similarly, a 20 cm mesh net has a circular diameter of 12.7 cm. Although this is slightly smaller than the head diameter of captive 4 mo old fur seals, it may well pose an entanglement threat for smaller animals.

At 17 months of age, the captive northern fur seals had average shoulder diameters of 23 cm. A 23 cm mesh net would therefore lodge tightly around the neck region but would not slip further down the body. Based on these dimensions, a net would have to have a stretched mesh size of 73 cm or more before a fur seal of this age could pass through a single mesh opening.

Scordino (1985) has shown that most webbing found on young seals weighs less than 150 g. He suggested that the high incidence of small debris entanglement may be due to the seals "playing" with small pieces of debris, as they do with kelp. This suggestion is supported by our observations of the fur seals' investigative nature when presented with net fragments. Prior to their first entanglement, all animals showed an immediate interest when they encountered a floating net and played with it almost continuously until they became entangled. While it is difficult to draw conclusions about the behavior of northern fur seals at sea from studies of a small number of captive animals, our observations nonetheless suggest that young fur seals are naturally inquisitive. Interestingly, however, these captive animals appeared indifferent to other floating objects (plastic bats, frisbees) that were occasionally placed in their tank.

Scordino's (1985) observations may also reflect a high incidence of at-sea mortality caused by entanglement in fragments larger than 150 g. Starvation, resulting from an increased energy demand during swimming, may be one consequence of entanglement in larger fragments. Previous studies have shown that entangled animals experience greater drag during swimming and that this drag increases exponentially with swim velocity and with greater net size (Feldkamp 1985). Because swimming energy requirements increase in relationship to drag, it was expected that metabolic increases would parallel increases in drag. Results from the swimming experiments support these predictions (Fig. 1; Table 2). At slow speeds, and with small (61 g and 100 g) nets, metabolism did not differ significantly from that measured at zero flow. At the higher speed of 1.1 m/s, metabolism was significantly elevated by both the 100 g and 200 g nets. With a 200 g net, animals visibly struggled against the 1.1 m/s flow. On several occasions, the experiment had to be stopped because of the fear of injury to the animal.

Metabolic rates at zero flow speeds and at 0.75 m/s were also higher during the winter experiments. This may be accounted for by differences in water temperature and body size. Miller (1978) has shown that the metabolic rate of northern fur seals increases linearly with decreasing water temperature. In 15°C water, animals in Miller's study had a metabolic rate of about 6.8 W/kg, close to the 6.95 W/kg (Table 2; no net, zero flow) measured for animals in this study. Under similar conditions during the spring, when water temperature had increased by 1.7°C, our measurements showed a 25% reduction in metabolic rate (Table 2).

This reduction in metabolic rate during the spring experiments was also observed for swimming and entangled animals. At 0.75 m/s in the winter, a 100 g net resulted in an average metabolic rate of 8.4 W/kg (Table 2). Under similar conditions during the spring, metabolism had dropped by 18%. Although the reasons for these metabolic changes are difficult to interpret, given the small sample size and changes in body mass, they do suggest, as did Miller (1978), that water temperature is an important factor influencing the energetic demands of swimming juvenile northern fur seals.

Metabolic rate measurements suggest that if juvenile northern fur seals become entangled in nets of 200 g or more, they will experience considerable difficulties in swimming and likely suffer a greater mortality than unentangled animals. Although our measurements were conducted over relatively slow swimming speeds, they do provide a basis of estimating the impact of entanglement on the energetic requirements of animals at sea. If animals with 200 g net fragments maintained an average speed of 1.1 m/s over the course of a day, they would need to consume 284 kcal of fish/kg body mass to maintain body weight. Using data on the caloric density of pollock (1.4 kcal/g) and on fur seal assimilation efficiencies (Miller 1978), this energetic requirement equals roughly 5 kg of pollock per day, compared with 1.9 kg for an unentangled animal. While it is likely that entangled fur seals would not swim constantly at sea, they may have to reach swim speeds higher than 1.1 m/s in order to catch prey, thereby increasing their metabolic expenditures. Moreover, water temperature of the Bering Sea is consider-

ably colder than that during the swimming trials. For these reasons, this value should be viewed as a minimum estimate of the energy required for survival by a juvenile fur seal entangled in a 200 g net.

The elevated swimming costs associated with entanglement and the resultant rise in food requirements suggest that northern fur seals enter a vicious cycle when entangled in larger fragments. As swimming costs increase, so will food demands. The need to capture more prey requires more swimming. Greater drag and perhaps reduced aquatic agility will undoubtedly lower capture success. Under these conditions, starvation would be a likely outcome.

The observation that northern fur seals virtually stopped swimming when entangled in 225 g nets is consistent with this scenario. By reducing the time spent swimming, fur seals should lower their energetic expenditures and hence their energy requirements. However, ADMR measurements before and during entanglement showed no significant differences. Since swimming activity declined by 75%, it is possible that the costs of resting and grooming were elevated by entanglement. A larger sample size would be needed to verify these findings. Nonetheless, grooming appeared to be much more vigorous and resting was not completely quiet. The fur seals often rested with both foreflippers submerged in the water, which may have elevated heat loss to the environment and led to greater energy requirements.

Fur seals were unable to free themselves from entanglement during the 2–3 d periods (Table 5). These results, however, must be interpreted with caution. Because fur seals were confined to a round holding tank with no haul-out areas provided, there were no objects present that might have caught the net and might have been used to remove it. From our observations, it is doubtful that animals could have freed themselves. However, Scordino (1985) has documented several instances where wild fur seals have lost their nets. It is possible that under natural conditions, fur seals might snag the encumbering fragment on rocks or other objects and be able to pull free.

The results of the present study show that juvenile northern fur seals are susceptible to, and adversely impacted by entanglement. Our captive fur seals were highly inquisitive and usually investigated and played with floating nets. Measurements of their head, neck, and shoulder diameters indicated that they were most susceptible to entanglement in nets with mesh sizes of 23 cm or more. Observations of actual entanglements substantiated this finding. Once entangled, northern fur seals virtually stopped swimming and spent considerably more time resting. However, energy expenditure did not drop accordingly, suggesting that the energy expended for grooming or resting may have been elevated by the presence of a net. Direct measurements also showed that at zero swimming speed, oxygen consumption was slightly, though not significantly, elevated because of the net. This elevation increased both with the size of the net and with increasing swimming speed. It is evident from these findings that net fragments of 200 g or more can lead to significant behavioral changes in captive northern fur seals and greatly influence their energy requirements during swimming.

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AN EXPERIMENTAL TRANSPLANT OF NORTHERN ABALONE, *HALIOTIS KAMTSCHATKANA*, IN BARKLEY SOUND, BRITISH COLUMBIA

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ABSTRACT

The biological and economic feasibilities of transplanting northern abalone, *Haliotis kamtschatkana* Jonas 1845, from exposed beds to two sites in sheltered, productive abalone habitat were investigated. After nine months, 39% and 72% of transplanted abalone were recovered at the two replicate sites. Recovery of tagged abalone at a control site, situated in the exposed source area, was 32%. Growth in shell length of transplanted abalone over the nine months averaged 7.8% whereas the average growth of non-transplanted controls was 3.7%, significantly less. There was little emigration of abalone from the transplant sites.

The study concludes that it is feasible to transplant 50–100 mm *H. kamtschatkana* in order to enhance growth. The economic feasibility of transplants is dependent on site-specific recovery rates and the costs of harvesting seed abalone. The population dynamics of abalone in exposed beds and the long-term potential for enhancing abalone settlement by introducing broodstock to depleted areas are two aspects which now require investigation.

The northern or pinto abalone, *Haliotis kamtschatkana* Jonas 1845, ranges from San Diego, CA to Sitka, AK (Mottet 1978); is most abundant in British Columbia and southeast Alaska; and is the only species of abalone found in British Columbia. Although present in the low intertidal zone in the northern part of its range, northern abalone are normally found subtidally to depths of 15 m (Cox 1962). In British Columbia the species is common in rocky habitats associated with surface kelps (*Macrocystis integrifolia* and *Nereocystis luetkeana*) at depths of 3–7 m.

In 1976 a market for Canadian abalone developed in Japan, and annual landings increased from less than 50 t (Farlinger and Bates 1985) to 425 t by 1978 (Breen 1980). Attempts were made to reduce the catch through effort control and the imposition of annual catch quotas. Despite these harvest restrictions, the northern abalone population in British Columbia has been extensively depleted and recruitment of legal-sized (>100 mm) abalone to the fishery is low (Breen 1980; Boutillier et al. 1984, 1985).

Although unharvested beds of legal size northern abalone are now uncommon, sublegal size abalone are often abundant in exposed habitats adjacent to once-productive commercial grounds. These smaller northern abalone are referred to as "surf" abalone by fishermen. They most often occur in beds of *Pterygophora californica* or under *Laminaria setchellii* cover. Breen (1980) estimated mean population densities of 9.5 abalone m^{-2} in seven beds of *Pterygophora* and 1.1 abalone m^{-2} in 20 beds of canopy-forming *Macrocystis*. However, only 3% of the abalone in the *Pterygophora* habitat were of legal size as compared with 46% in *Macrocystis* habitat. In exposed areas, northern abalone may be slow-growing and never reach legal size because of food limitation. Alternatively, these northern abalone may grow at normal rates but experience high rates of mortality, or emigrate to other habitats.

Breen (1986) transplanted 617 sublegal size *H. kamtschatkana* from exposed habitat in the Queen Charlotte Islands to a more sheltered *Macrocystis* community. Recovery after one year was 10%, and the author concluded that growth of these "surf" abalone was enhanced when transplanted to more favorable habitat. The present study examines the feasibility of transplanting large numbers of sublegal size northern abalone from an exposed area to more sheltered habitats. Specific goals were 1) to determine the growth of transplanted individuals relative to nontransplanted controls, 2) to monitor the recovery of northern abalone in transplant and control areas after approximately one year, and 3) to assess the economic feasibility of transplanting sublegal size northern abalone for subsequent commercial harvest.

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MATERIALS AND METHODS

Study Sites

Study sites were located in Barkley Sound on the west coast of Vancouver Island (Fig. 1). Sublegal size northern abalone were removed from 5 km of exposed shoreline at the entrance to Barkley Sound (source area), and these abalone were transplanted to site A on Fleming Island and site B on Tzartus Island, 10–12 km towards the head of Barkley Sound from the source area. For the purposes of this study, sublegal size northern abalone are defined as 50–99 mm in length. These individuals should recruit to the fishery within 0–3 years, given suitable habitat.

An exposed rocky pinnacle (site C) within the source area was designated as a control site to measure growth and recovery of nontransplanted northern abalone. The three study sites were isolated by natural features (e.g., sand) from nearby abalone habitat to minimize immigration or emigration.

The source area consisted of a series of rocky headlands and bays. The habitat of the headlands and control site was typical of exposed rocky outcrops on the west coast of Vancouver Island. At the control site, a 2 m band of vegetation (*Lessoniopsis littoralis* and *Laminaria groenlandica*) formed the lower intertidal zone, and northern abalone and sea urchins, *Strongylocentrotus franciscanus*, occurred below this zone on a rocky reef dominated by encrusting coralline algae. Bays in the source area were sloped less steeply and contained beds of *Nereocystis luetkeana* and *Pterygophora californica*. Transplanted northern abalone were collected from both headland and bay habitats in the source area.

Both transplant sites were located in and directly below beds of *Macrocystis integrifolia* situated on isolated rocky reefs. Sites were defined by marking 60 m wide × 8 m deep sections of these beds with a weighted line at each lateral boundary. The *Macrocystis* bed at site A was 2–5 m wide, bordered by a deeper 3 m wide band of brown algae, *Desmarestia ligulata*. The substrate at this site was steeply sloped bedrock. Large boulders, covered by *P. californica* and encrusting coralline algae, occurred at the base of the bedrock slope. Sea urchins (*S. franciscanus* and *S. purpuratus*) occurred below the vegetation zone to a depth of 8 m. At deeper depths the bottom was composed of sand, isolated cobbles, and boulders.

At site B, the *Macrocystis* zone was 6–8 m wide and bounded at the lower edge by kelps (*Laminaria saccharina*, *P. californica*, and *Agarum fimbriatum*). *Desmarestia ligulata*, although present, did not form a distinct zone as at site A. The bedrock substrate was sloped less steeply than at site A and was overlain with loose cobbles. At deeper depths, sand was the primary substrate. As at site A, sea urchins were present below the vegetation zone.

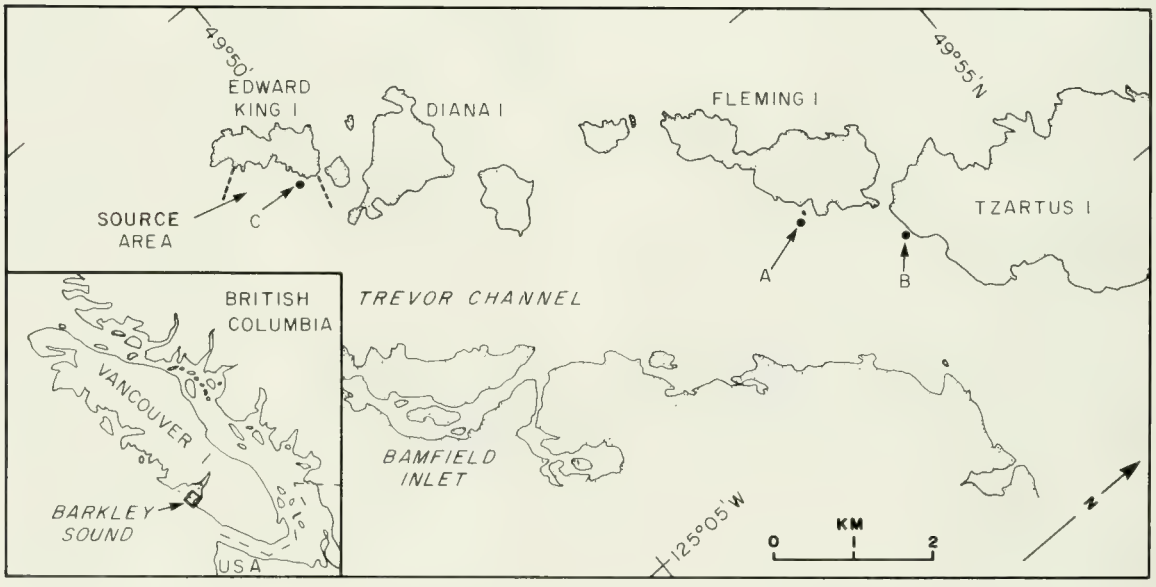

FIGURE 1.—Location of the study sites in Barkley Sound on the west coast of Vancouver Island.

Removal, Tagging, and Transplanting

Prior to transplanting any northern abalone, divers searched for and removed indigenous abalone from the transplant sites. The divers then collected the abalone from the source area using a dull knife or the arm of the sea star, *Pycnopodia helianthoides*. The arms elicit an escape response, which allows the abalone to be hand-picked without damaging the foot. Tagging and transplanting were conducted from mid-June to July 1984. Approximately 20% of the northern abalone, selected haphazardly, were tagged with individually numbered, stainless steel washers immediately after capture. A loop of stainless steel wire was inserted through the last two respiratory pores of the abalone shell, a washer tag was added to one end of the loop, and the wire was then twisted with a pair of pliers to anchor the tag against the abalone shell. Length, width, and sex of all tagged northern abalone were recorded. Shell lengths of a subsample (10%) of untagged abalone were measured for comparison with the tagged samples. Tagged abalone were placed between layers of moist kelp so that the tag wires did not damage overlying abalone. Abalone were then transported to transplant sites within 3–4 hours of harvest and placed by divers in or immediately below the *Macrocystis* zone, the preferred habitat for adult abalone in sheltered locations (Breen 1986). A total of 502 tagged abalone were placed at site A and 506 at site B. Abalone (n = 438) were also removed from the control site (C), tagged and replaced onto the site within 2–3 hours.

Divers searched the transplant sites within 48 hours of completing the transplant, and monthly from August 1984 to February 1985. All tagged and untagged abalone shells found in the study sites were collected.

Recovery of Transplanted Abalone

In March 1985, divers harvested tagged and untagged northern abalone at the transplant sites and tagged abalone at the control site. To maximize recovery, divers divided each site into a series of 5 m sections using cinder blocks and cord. The area of each section was measured and divers then searched repetitively for abalone within each section. Harvesting was terminated when repetitive searches in each area recovered less than 5% of the abalone harvested in the initial search. Divers also searched areas adjacent to the study site for tagged abalone to establish the magnitude and distance of emigration. Length, width, and sex of recovered, tagged abalone were recorded, along with the lengths of all tagged abalone.

RESULTS

Abalone Transplants

A total of 2,737 northern abalone were transplanted to site A and 2,677 abalone were transplanted to site B (Table 1). The mean length of tagged abalone transplanted to site A was 88.7 mm and to site B, 90.2 mm. The mean length of abalone tagged at the control site (site C) was 78.7 mm. The differences in mean length between sites were all significant ($P < 0.05$). The mean length ($\pm$SD) of subsamples of untagged abalone transplanted to sites A and B were 84.6 + 12.8 mm (n = 204) and 8.8 $\pm$ 11.5 mm (n = 257), respectively.

TABLE 1.—Summary of number and mean length of abalone at each site. Density for site C is estimated from random quadrat surveys conducted prior to tagging ($\pm$ SD).

Site	Study area (m^2)	Number transplanted	Density (abalone m^{-2})	Tagged abalone n	Tagged abalone $\bar{x}$ (mm)	Tagged abalone SD (mm)
A (transplant)	550	2,737	4.98	502	88.7	11.5
B (transplant)	590	2,677	4.54	509	90.2	9.8
C (control)	1,800	—	0.56 $\pm$ 0.91	438	78.7	11.0

Although divers carefully placed each transplanted northern abalone foot down in suitable rock crevices or loose rock within the study areas, many abalone subsequently moved outside the lower boundary of the sites to depths of 7–10 m. This movement made the effective area of the transplant sites about three times larger than the original 60 m × 8 m dimensions. Little lateral movement of northern abalone beyond the boundaries of the study sites was observed.

At sites B and C, the recovery of tagged shells by monthly diving inspections was highest in August, one month after the transplant (Fig. 2). Recovery of both tagged and untagged shells at all sites in early July suggests that mortality one week after transplanting was less than 2%. The relatively high recovery of tagged shells in March 1985 was probably a consequence of the more intensive searching effort during the final harvest. Cumulative recoveries of tagged shells were 10.5% at site A, 18.0% at

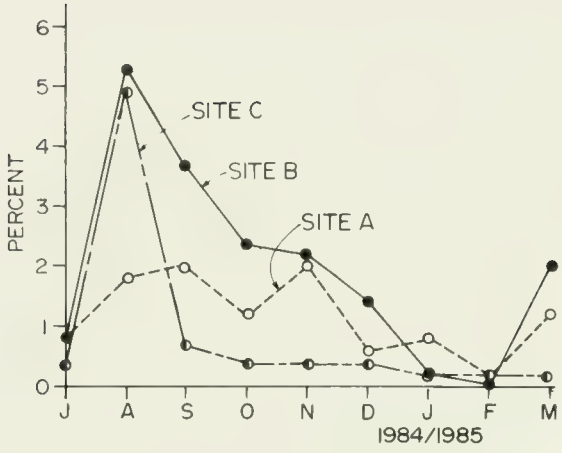

FIGURE 2.—Monthly recovery of tagged shells and tagged shell fragments from dead abalone. Results expressed as the percentage of the original number of tagged abalone.

site B, and 7.2% at site C (expressed as a percentage of the original tagged number).

Predation and Seasonal Variation in Habitat

Shells recovered during monthly inspections were categorized by the nature of breakage. Shells present on the sites prior to the transplant were not categorized. These older shells were identifiable by degree of shell deterioration and epiphytization. Most shells were recovered whole: 68% at site A, 51% at site B, and 79% at site C.

Recoveries of loose tags owing to tag loss or predation ranged from 0% of the initial tagged population at site C to 1.3% at site B. The relative proportion of loose tags recovered at each site corresponded to the proportion of broken shells at each site, suggesting that shell breakage due to predation may be the main cause of loose tags.

One to three octopus dens were present at each site. Abalone shells found outside the dens were unbroken and not drilled. Over the course of this study, four octopuses were removed from site A, two from site B, and one from site C. Dens were often reoccupied three to four months after removal. Red rock crab, *Cancer productus*, were also a numerically important prey item of octopus at the study sites.

In July and August, the sunflower star, *Pycnopodia helianthoides*, preyed intensively on abalone at the transplant sites. This species was seen to prey on weakened or stressed abalone, and starfish were observed actively feeding on abalone immediately following the transplant. As with octopus, shells of abalone eaten by *P. helianthoides* were always recovered unbroken, either under actively feeding stars or entirely within the stomach.

In contrast, broken or chipped shells were presumed to be due to predation by red rock crabs, wolfeels (*Anarrhichthys ocellatus*), or cabezons (*Scorpaenichthys marmoratus*). Red rock crabs were abundant during the spring and summer at all sites except site C, but were rarer in the fall and winter. A few abalone shells were recovered outside a wolfeel den at site A, and one or two cabezon were observed at all sites throughout the study period.

Considerable seasonal variation in the marine plant community at the transplant sites was observed. Annuals, such as *Desmarestia ligulata*, died back in October and were completely gone by November. The *Macrocystis* canopy was also reduced in fall and winter as a result of storm damage. Plants at site A were stripped of most fronds over the winter while losses were lower at site B, the more sheltered of the two transplant sites. Holdfasts remained intact and growth was renewed by March.

Recovery of Abalone

After nine months, 72% of the transplanted northern abalone were recovered from site A, and 39% from site B (Table 2). When shells from dead northern abalone collected during the 9-mo period were included, 88% of abalone at site A and 55% of abalone at site B could be accounted for. At the control site (C), 31% of the tagged abalone were recovered live and 40% of the original tagged abalone could be accounted for by including tagged shells recovered over the study period. The difference in percent recovery between the two transplant sites suggests that either abalone survival, abalone movement, or the ability of divers to find abalone differed between the sites.

The recovery of tagged northern abalone was 6% less than recovery of untagged abalone at both transplant sites (Table 2), and the ratio of tagged to untagged abalone at recovery (0.20) was less than the initial ratio of 0.23. This difference is not significant (χ^2 analysis, $P < 0.05$), indicating that losses due to the tagging procedure were minimal.

The number of tagged shells recovered by divers over the 9-mo study allowed estimation of minimal instantaneous natural mortality (M_{min}) (Ricker 1975). This calculation assumes that divers recov-

TABLE 2.—Recovery of live abalone in March 1985, recovery of abalone shells over the study period, and estimation of M_{min} (from tagged shell recovery) and M_{max} (from live tagged abalone recovery). Number recovered was after 9 months, so $M = -\ln\left(\frac{\#\text{ tagged survivors}}{\#\text{ initially tagged}}\right) \cdot \frac{12}{9}$.

Site	Initial number		Recovery				% live recovery			M	
			tagged		untagged						
	tagged	untagged	shells	live	shells	live	tagged	untagged	Total	M_{min}	M_{max}
A (transplant)	502	2,235	53	330	396	1,628	66	73	72	0.15	0.56
B (transplant)	509	2,168	92	175	353	861	34	40	39	0.27	1.42
C (control)	438	—	33	141	—	—	31	—	31	0.10	1.51

ered the shells of all tagged northern abalone that had died. The recovery of live tagged abalone allows estimation of maximal instantaneous natural mortality (M_{max}), assuming that divers recovered all the living abalone. Values for M_{min} ranged from 0.10 to 0.27 for the three study sites; M_{max} ranged from 0.56 to 1.51 (Table 2).

The movement of northern abalone from the lower edge of the *Macrocystis* bed to deeper (5–11 m) water shortly after the transplant (described above) effectively increased the area of each transplant site by threefold. Approximately 30% of recovered northern abalone were found below the vegetation zone at both transplant sites. This movement, coupled with abalone losses, resulted in final abalone densities of 1.27 m^{-2} at site A and 0.73 m^{-2} at site B.

Prior to final harvesting, divers searched beyond the expanded boundaries of the sites for tagged northern abalone. Little lateral movement of northern abalone along the shoreline had occurred. At site A, 11 tagged abalone (2.2% of the original tagged number) were found outside the study area. Maximum distance from the site was 37 m, and one tagged abalone was found at a depth of 18 m. At site B, three tagged abalone were found outside the site area, all in deeper water. The most extensive movement was recorded at the control site. Ten tagged abalone (2.2% of the tagged population) were recovered outside the site boundaries; one abalone had moved 125 m; and three abalone had crossed a 50 m wide sandy channel.

At sites B and C, a considerable proportion of the transplanted or tagged population could not be accounted for. The low recovery of tagged abalone outside the boundaries of the sites suggests that emigration is not the sole explanation. However, searches conducted outside the site boundaries were less intensive than those conducted within.

Growth

Figure 3 gives the length frequencies of tagged northern abalone at each site at the initiation of the study in June 1984 and upon recovery in March 1985. Differences between mean initial and final lengths at each site were, in all cases, significantly different (paired t-test, $P < 0.05$). The mean growth of tagged northern abalone after 9 months was 7.1 mm at site A, 7.2 mm at site B, and 2.9 mm at site C, the control site. Mean growth of untagged northern abalone was 9.4 mm at site A and 9.9 mm at site B.

Growth rates of northern abalone were analyzed by Walford plots, in which the initial length of individual tagged abalone (l_0) are plotted against the length of the same individual at recovery in March 1985, 9 months later (l_1). The numbers of data pairs were 306, 167, and 126 at sites A, B, and C, respectively. Table 3 summarizes parameters of the regression lines of Walford plots for each site as well as the annual Brody coefficient and asymptotic length calculated from these regression parameters (Ricker 1975). The annual Brody coefficient varied from 0.178 to 0.440, and was lowest at the control site. Values for asymptotic length varied from 104 to 112 mm, also being lowest at the control site.

TABLE 3.—Parameters for linear regression, annual Brody coefficient (K), and asymptotic length (l_∞) as calculated from Walford plots.

Site	Linear regression					l_∞ (mm)
	N	a	b	r^2	K	
A (transplant)	306	30.8	0.719	0.64	0.440	110
B (transplant)	167	24.8	0.779	0.76	0.333	112
C (control)	126	13.0	0.875	0.87	0.178	104

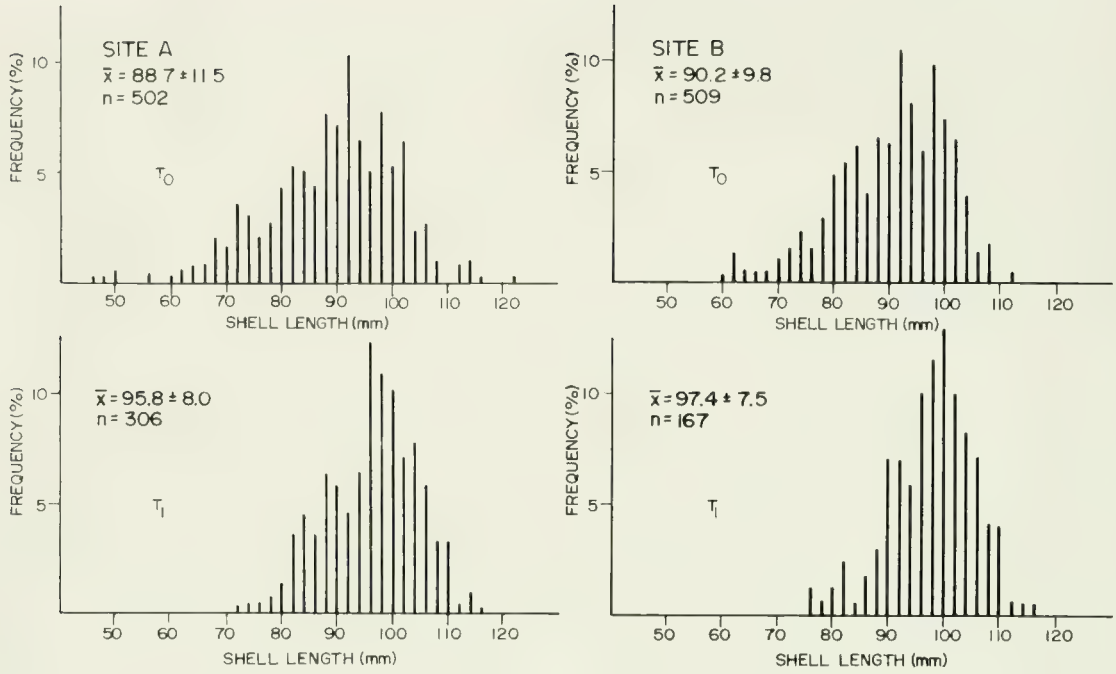

FIGURE 3.—Length frequencies of tagged abalone at each site at the beginning (June 1984 - T_0) and at end

Growth of northern abalone at the transplant and control sites was compared by using the Walford regression to estimate final lengths and associated confidence intervals for abalone of initial lengths equal to the lower (75 mm) and upper (100 mm) size range of abalone placed at the two transplant sites (Table 4). As confidence intervals are narrowest at the mean value of l_0, between site comparisons using these more extreme values are more rigorous than using l_0 values which fall between 75 and 100 mm. The hypothesis that predicted l_1 values at l_0 = 75 and 100 mm for transplanted northern abalone are greater than the corresponding l_1 value for control abalone was then tested (one tailed t-test). All differences were significant at $P < 0.05$ (Table 4), indicating that northern abalone growth was significantly greater for abalone transplanted to sites A and B as compared with nontransplanted abalone at the control site.

TABLE 4.—Estimates of growth calculated from Walford plots for abalone for the lower (75 mm) and upper (100 mm) size range of transplanted abalone. Values are expressed ±95% confidence interval. l_0 = length at initiation of study, l_1 = length after nine months. Values in parentheses are t – statistic and degrees of freedom comparing the l_1 values at each transplant site with the corresponding l_1 values at the control site. $P < 0.05$ in all cases.

	Length after 9 months t_1 (l_1)	
Site	l_0 = 75 mm	l_0 = 100 mm
A (transplant)	84.7 ± 0.7 (16.22, 305)	102.7 ± 0.5 (7.97, 305)
B (transplant)	83.3 ± 0.9 (10.02, 166)	102.8 ± 0.5 (8.85, 166)
C (control)	78.6 ± 0.4	100.5 ± 1.0

Economic Feasibility

The economic feasibility of transplanting wild northern abalone seed for subsequent commercial harvest depends primarily on three factors: 1) the cost to collect and transplant stock, 2) the rate of recovery of legal-sized abalone after a suitable growing period, and 3) the price of abalone. The first factor depends on abalone density in the source area and the distance to the transplant sites. The present study shows that the second factor (recovery rate) can vary greatly between sites.

In this study 6 diver-days were required to collect 5,000 sublegal-sized northern abalone at the source area and move them to the transplant sites. This variable cost was estimated to be $1,500, at a rate of $250 diver-day^{-1} for wages and fuel costs.

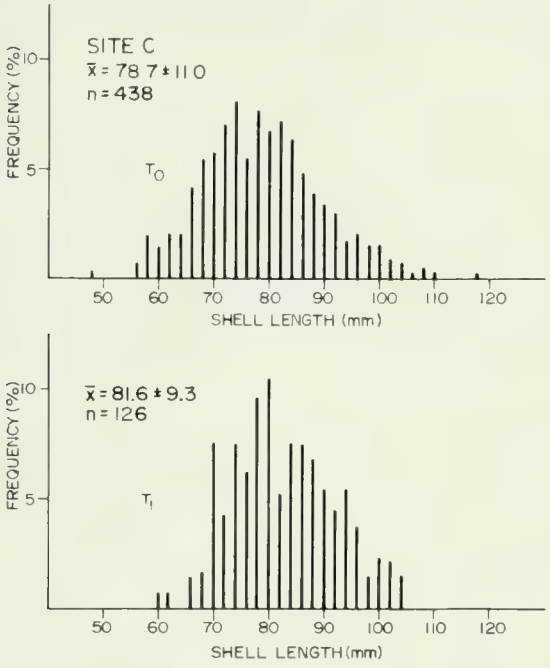

FIGURE 3.—*Continued*—(March 1985 - T_1) of the study.

Harvest costs were similarly estimated at \$1,575. Fixed costs were not included and were assumed to be zero. This information is used in the following simple economic model which examines the rate of economic return as a function of M_{max} (instantaneous natural mortality estimated from recovery of live abalone).

Assuming that 5,000, 80 mm abalone are transplanted, they reach legal size (100 mm and 340 g) in two years, and can be sold at a price of \$11 kg^{-1}. Then

gross return = \$11 kg^{-1} × 0.34 kg $abalone^{-1}$ × 5,000 abalone × e^{-tM}, where t = 2, M = M_{max}

net return = gross return-harvest costs, where harvest costs = \$1,575

profit = net return-initial costs, where initial costs = \$1,500

discounted profit = net return $\left(\frac{1}{1+d}\right)^t$ − initial costs, where d = discount rate = 10%

internal rate of return (IRR) = $e^{\text{return rate}}$ − 1.0, where return rate = (ln (net return/initial costs))/t.

Table 5 summarizes these economic parameters for values of M_{max} ranging from 0.10 to 1.00. These data indicate that a reasonable value for the internal rate of return (i.e., >20%) would be obtained at M_{max} values of 0.80 or less. Transplants to site A but not site B would show a reasonable rate of return.

This model can be generalized to estimate economic returns for variable abalone seed costs in the case of transplanting hatchery-reared seed to the wild. Figure 4 summarizes internal rates of return for 20 mm hatchery seed of variable cost, a 4.5 yr growth period, planting costs of \$0.20 per abalone, and harvest costs of \$0.40 per kg. All other assumptions are the same as the model given above. Under these price assumptions, M_{max} values must be less than 0.6 to show a reasonable rate of return if seed costs are ≤\$0.10 per abalone. At M_{max} values greater than 0.8, transplanted abalone seed will not yield a reasonable rate of return unless seed costs are extremely low (<\$0.02 per abalone).

TABLE 5.—Summary of economic returns from transplanting abalone, assuming 2 years to recovery. Calculated from the economic model given in text. IRR = Internal rate of return; t = 2 years.

M_{max}	Profit	Discounted profit	IRR (× 100%)
0.10	\$12,235	\$9,865	203
0.20	9,460	7,553	171
0.40	5,328	4,139	113
0.60	2,557	1,851	64.8
0.80	700	318	21.4
0.90	16	−250	0.8
1.00	−544	−710	—

DISCUSSION

In this study northern abalone transplanted from exposed areas to more sheltered habitat grew faster than nontransplanted controls. These results corroborate the observations of Breen (1986) that "surf" abalone retain the potential to grow well when placed in more productive habitat. These observations suggest that abalone are, to some degree, food limited in exposed habitats which have little to no canopy-forming algae.

Because northern abalone varied in size in different sections of the source area, the initial size of nontransplanted abalone at the control site was significantly less than that of the transplanted abalone (Fig. 3). This bias would be expected to reduce the difference in growth rate between the abalone at

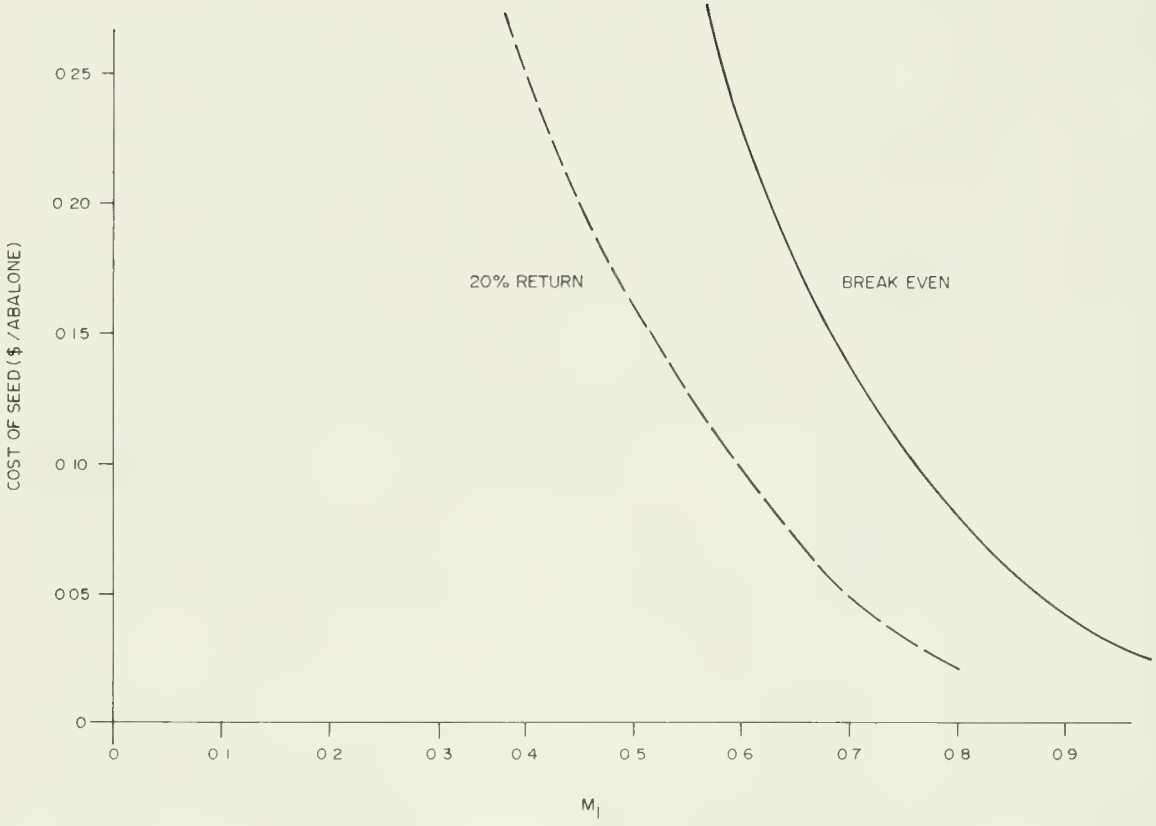

FIGURE 4.—Isoprofit lines drawn from internal rates of return calculated at varying seed cost and natural mortality values. Solid line = breakeven point, dotted line = 20% internal rate of return.

the control and transplant sites, because growth rate is inversely related to body size. Therefore the growth rate differences observed in this study are likely smaller than would have been observed if the mean length of transplanted abalone had been equal to the mean length of the control group at the initiation of the study. Analyzing growth rates by Walford plots diminishes this bias because the analysis compares the length of individual abalone at the beginning and end of the study period and does not use pooled data to compare growth rates among sites.

In most transplant experiments, recovery following transplanting depends on both abalone size and source and is greatest with larger abalone collected from the wild. In the present study wild-harvested northern abalone of 50–100 mm length were transplanted, and recovery was 72% and 39% at the two sites 9 months after the transplant. Saito (1984) reported 18% recovery 9 months after transplanting 25 mm hatchery-reared *Haliotis discus hannai* in Japan. The author also stated that commercial recapture rates are 5–10% for hatchery-reared seed and 20–25% for wild seed. Recovery of 45–71 mm, hatchery-reared *Haliotis rufescens* in California was less than 1% one year after transplanting (Tegner and Butler 1985). Inoue (1976) reported increased survival with increasing seed size up to 70 mm. Tegner (pers. commun.)[2] estimated an annual mortality rate of 9.1% for mature, native green abalone, *Haliotis fulgens*, one year after being transplanted in California. The use of large, wild-harvested northern abalone likely contributed to the relatively high recovery rates observed in the present study.

The markedly different rates of recovery between the two transplant sites seemed independent of handling, tagging, and transplant procedures. Shells collected within two weeks of release indicated that immediate posthandling mortality was similar (<2%)

[3]M. J. Tegner, Scripps Institution of Oceanography, La Jolla, CA 92092, pers. commun. January 1987.

at all sites. The similar ratio of tagged to untagged northern abalone at the initiation and end of the study demonstrated that both tagged and untagged animals had similar survival rates.

Breen (1986) calculated M, from population size structure and growth rate estimates, to be 0.05–0.24 for *H. kamtschatkana* at eight sites in British Columbia. These values are consistent with estimates of M, derived from a variety of techniques, of 0.05–0.40 for abalone populations in Australia and New Zealand (Shepherd et al. 1982; Sainsbury 1982). In California, estimates of M (partly based on dead shell recovery) are higher, ranging from 0.36 to ∞ for four native species of *Haliotis* (Tutshulte 1976; Hines and Pearse 1982). The highest estimates are from areas that experience sea otter, *Enhydra lutris*, predation. Estimates of M calculated from data given by Tegner and Butler (1985) are 0.40 and 0.55 for two transplanted populations of red abalone, *H. rufescens*.

In the present study, estimates of M based on recovered, tagged shells (M_{min}) are similar to values determined for abalone populations from similar latitudes in British Columbia (Breen 1986) and southern Australia (Shepherd et al. 1982). Values of M determined from the recovery rate of live abalone (M_{max}) are higher than most values of M reported in the literature. It is likely that M_{max} estimates of instantaneous natural mortality are high because some abalone probably emigrated or remained hidden within the sites. However, while unrecovered abalone would still be able to contribute to population reproduction, they would not likely be available for harvest; the after-harvest population density would be too low to encourage the return of fishermen, and the animals might remain well hidden. Effectively, these abalone can be considered removed from the harvestable biomass, and since there are only two categories, available and unavailable animals, in most cost-benefit and/or exploitation models, unrecoverable abalone should be considered unavailable abalone. For this reason M_{max} is an appropriate term for use in models assessing the economic feasibility of abalone transplants and in other situations where animals are established in an area for the purpose of future exploitation.

A considerable proportion of tagged and/or transplanted northern abalone were unaccounted for at sites B and C. The difference in percent recovery of live abalone at the two transplant sites (72% versus 39%) was due primarily to these abalone, as approximately the same number of shells were collected at each site. There are several explanations: 1) difficulty in locating abalone due to complex bottom topography, 2) physical removal of abalone from the site by mobile predators such as octopus and sea stars, 3) the destruction of shells by predators such as crabs, 4) emigration, and 5) transport of shells from the site by waves or currents.

In California, Tegner and Butler (1985) attributed abalone loss during transplant experiments to both predation and emigration, citing the recovery of shells in all directions outside the study site as evidence of random dispersal of live animals. In the present study, searches outside the sites at the termination of the study suggested little emigration of tagged abalone, except at the control site. Although no studies have been done on the natural movement of *Haliotis kamtschatkana*, the mean distance moved in a year by tagged ormers (*Haliotis tuberculata*) in France was only 6.7 m for the 68% of the population that showed any evidence of movement (Clavier and Richard 1984). That study also showed that smaller abalone tended to be less mobile. Hines and Pearse (1982) reported that marked abalone shells drifted 2–3 m in three months. The degree of shell drift due to wind or current action is obviously site specific and probably only occurred at the more exposed control site in the present study.

Three fundamental questions concerning the feasibility and benefit of transplanting abalone from exposed areas remain: 1) the number and extent of abalone in exposed coastal areas has not been established, 2) the population dynamics and the reproductive contribution from such populations to the total coastal stock remain unknown, and 3) the potential of transplanted abalone to enhance population reproduction and ultimately recruitment at specific transplant sites has to be determined on a site-by-site basis.

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COMPARISON OF SOME GENERA AND SPECIES OF BOX CRABS (BRACHYURA: CALAPPIDAE), SOUTHWESTERN NORTH ATLANTIC, WITH DESCRIPTION OF A NEW GENUS AND SPECIES

Austin B. Williams[1] and C. Allan Child[2]

ABSTRACT

Five species of calappid crabs from the southwestern Atlantic that belong to the genera *Calappa*, *Cyclozodion* new genus, and *Paracyclois* are analyzed on the basis of morphology, morphometrics, geographic, and bathymetric range. *Calappa tortugae*, new rank, known in the past as *C. angusta* in the broad sense, is restricted and compared with its eastern Pacific twin species, *C. saussurei*. Two small species placed in *Cyclozodion* were until now unrecognized and partly included in *Calappa angusta*, broad sense. *Cyclozodion angustum*, a relatively smooth form, is the type species of the new genus, and *C. tuberatum*, a rough form superficially resembling *Calappa tortugae*, is described as new. Species of both *Paracyclois* and the Early Tertiary genus *Calappilia* in which it was subsumed are reviewed, the former is revalidated, and its only two species, western Atlantic *P. atlantis* and western Indo-Pacific *P. milneedwardsii*, are rediagnosed. Diagnoses and discriminations are accompanied by illustrations. Keys to calappid genera in the Western Atlantic, and for identification of *Cyclozodion* and *Paracyclois* species are given.

Holthuis (1958) revised five species of West Indian box crabs, *Calappa cinerea* Holthuis 1958, *C. flammea* (Herbst 1794), *C. nitida* Holthuis 1958, *C. ocellata* Holthuis 1958, and *C. sulcata* Rathbun 1898, but a species from that region known until now as *C. angusta* A. Milne Edwards 1880 was not included in his paper because the collection he studied included no representatives of that form. We find that this latter species is not at all well defined, and the purpose of this paper is to clarify its status and that of similar species in related genera.

Samples of decapod crustaceans from exploratory trawling by the Bureau of Commercial Fisheries RV *Pelican*, U.S. Fish and Wildlife Service RV *Combat*, National Marine Fisheries Service RV *Silver Bay*, RV *Oregon*, and RV *Oregon II* deposited in the crustacean collection of the National Museum of Natural History (USNM), Smithsonian Institution, contain specimens of a seldom reported calappid crab, *Paracyclois atlantis* Chace 1939, 1940 from the Caribbean region of the western North Atlantic, and representatives of a genus not previously recognized. Two small calappid species in the catalogued USNM crustacean collection have been attributed to *Calappa angusta* A. Milne Edwards 1880 by Rathbun (1937) and other authors (see Williams 1984) on the basis of what were thought to be juvenile characters exhibited by the carapace of that species. Review of the material in the USNM shows this concept to be in error. Moreover, representatives of the extant type series of *C. angusta* in the Museum of Comparative Zoology (MCZ), Harvard University, consist of very small juveniles, a holotype and four paratypes in which definitive characters are poorly developed, that surprisingly belong not to one but three calappid species. "*Calappa angusta*" as presently understood is in reality a complex of species belonging in *Calappa* Weber 1895 and the previously unrecognized genus.

Only two species of *Paracyclois* Miers 1886 have been described, the above mentioned, and the type species, *P. milneedwardsii* Miers 1886, from the western Indo-Pacific. Glaessner (1969) synonymized *Paraclyclois* with *Calappilia* A. Milne Edwards 1873, considered until that time to include only species of Middle Eocene to Upper Oligocene ages in North America, Europe, and the East Indian region, but did not discuss reasons for his action. Because our determinations involved generic placement of material from trawl samples, we reviewed literature concerned with both of these genera and studied specimens of selected species of *Calappilia* in the fossil crustacean collection of the USNM. Austin B. Williams developed the text, C. Allan Child rendered the drawings, and both of us identified and cross-checked material.

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Key to Recent genera of Calappidae in the western Atlantic Ocean

1. Chelae essentially symmetrical, no unusually enlarged teeth or protuberances, Subfamily Matutinae 2
   Chelae dissimilar, major chela with large tooth on dactyl and pair of protuberances on propodus, Subfamily Calappinae 3

2. Carapace considerably broader than long, regularly convex above ..... *Hepatus* Latreille 1802
   Carapace nearly as long as broad, dorsal surface uneven ..... *Osachila* Stimpson 1871

3. Posterolateral region of carapace not expanded into dentate, winglike projection 4
   Posterolateral region of carapace expanded into dentate, winglike projection 5

4. Merus of cheliped bispinous on distal outer surface, with lower spine strong and greatly extended laterally ..... *Acanthocarpus* Stimpson 1871
   Merus of cheliped not bispinous on distal outer surface, carapace subcircular, small spine at lateral angle ..... *Cycloes* De Haan 1837

5. Pereopod 5 with articles spineless 6
   Pereopod 5 with row of spines on flexor surface of ischium-merus ..... *Paracyclois* Miers 1886

6. Greatest span of winglike posterolateral projections less than maximal span between anterolateral margins; outer proximolateral corner of palm bearing short, flattened, smoothly crested ridge ..... *Cyclozodion* new genus
   Greatest span of winglike posterolateral projections exceeding maximal span between anterolateral margins; outer proximolateral corner of palm bearing flattened acute spine or subrectangular ridge ..... *Calappa* Weber 1795

***Calappa tortugae* Rathbun 1933, new rank**

Figures 1, 2

Calappa saussurei tortugae Rathbun 1933:183.
Calappa angusta.—(Part, not selected juveniles.) A. Milne Edwards 1880:18.—Hay and Shore 1918: 421, pl. 31, fig. 7.—Rathbun 1937:210, pl. 64, figs. 4–6.—Chace 1956:18 (list).—Williams 1965:154, fig. 134; 1984:273, fig. 203.—Pequegnat 1970: 177.—Powers 1977:30.

Material studied.—Specimen lots in USNM recorded by Rathbun (1937) under *C. angusta* and *C. saussurei tortugae* (catalog numbers only) plus material added since that time.

North Carolina: USNM 68530.—101676. 1 ♂, 1♀ (juv.); 34°18′N, 75°58′W, SE off Cape Lookout, 137 m; *Combat* stn. 405, 21 June 1957.—101675. 1 ♂; 34°19′N, 75°54′W, SE off Cape Lookout, 183 m; *Combat* stn. 402, 21 June 1957.—202745. 1 ♂, 2 ♀; 33°48′48″N, 76°34′24″W, 46 m; BLM, 4 Mar. 1981.—202746. 1 ♀; 33°48′12″N, 76°34′24″W, 116 m; Duke Univ. for BLM, 14 May 1981.—202747. 1♀ (ovig.); 33°47′36″N, 76°34′24″W, 116 m; Duke Univ. for BLM. 14 May 1981.—202748. 1 ♂; 33°48′06″N, 76°34′24″W, 105 m; Duke Univ. for BLM, 14 May 1981.—202749. 1♂; 33°48′42″N, 76°34′12″W, 102 m; Duke Univ. for BLM, 14 May 1981.—202750. 1 ♀ (juv.); 33°48′42″N, 76°34′30″W, 99 m; Duke Univ. for BLM, 14 May 1981.—220962. 1 ♂, 3 ♀; 33°48′36″N, 76°34′06″W, 69 m; Duke Univ. for MMS, 4 Mar. 1981.

South Carolina: 188682. 2 ♂, 1 ♀; 32°18′30″N, 79°00′30″W, 84 m; *Dolphin* 577096, 3/4 Yankee trawl, MARMAP, 9 Mar. 1977.—188677. 1 ♂; 33° 17′N, 77°08′42″W, 155 m; *Dolphin* 573426, 3/4 Yankee trawl, MARMAP, 15 Nov. 1973.—*Silver Bay* stn. 2263. 2 ♂; E of Charleston, 33°04′N, 78° 12′W, 29 m; trawl, 28 July 1960.

Georgia: 155583. 1 ♂; 30°50′30″N, 80°01′W, 93 m; M. Gray 209, 7 May 1963.—155582. 3 ♂; 30° 55′30″N, 79°57′W, 91–119 m; M. Gray, 12 June 1963.—188680. 1 undet.; 31°43′30″N, 79°38′30″W, 64 m; *Dolphin* 576078, 3/4 Yankee trawl, MARMAP, 5 May 1976.

Florida: 66382. *C. saussurei tortugae* holotype, ♂; Tortugas, about 12 mi S Red no 2 Buoy, 110 m, W. L. Schmitt, stn. 33–31, 22 July 1931.—66381. 1 ♀; same.—234461. 1 ♂, 5 ♀; same.—68506, 68507, 68508, 68509, 68515, 71369.—101413. 6 ♂, 3 ♀; off Jacksonville, 30°11′N, 80°17′W, 59 m; *Combat* stn. 72, 31 Aug. 1956.—101414. 2 ♂, 1 ♀; SE Cape Canaveral, 28°32′N, 80°05′W, 119 m; *Combat* stn. 90, 3 Sept. 1956.—91137. 1 ♂, 1 ♀; W Cape Romano, 25°35′N, 83°42′W, 110 m; *Oregon* stn. 35, 26 June 1950.— 97487. 1 ♂; SW Sarasota, 27°07′N, 83°19′ W, 42 m; *Oregon* stn. 963, 4 Apr. 1954.—101678. 1 ♂; S Cape San Blas, 29°10′N, 85°48′W, 101–130 m; *Silver Bay* stn. 100, 26 July 1957.—*Silver Bay*

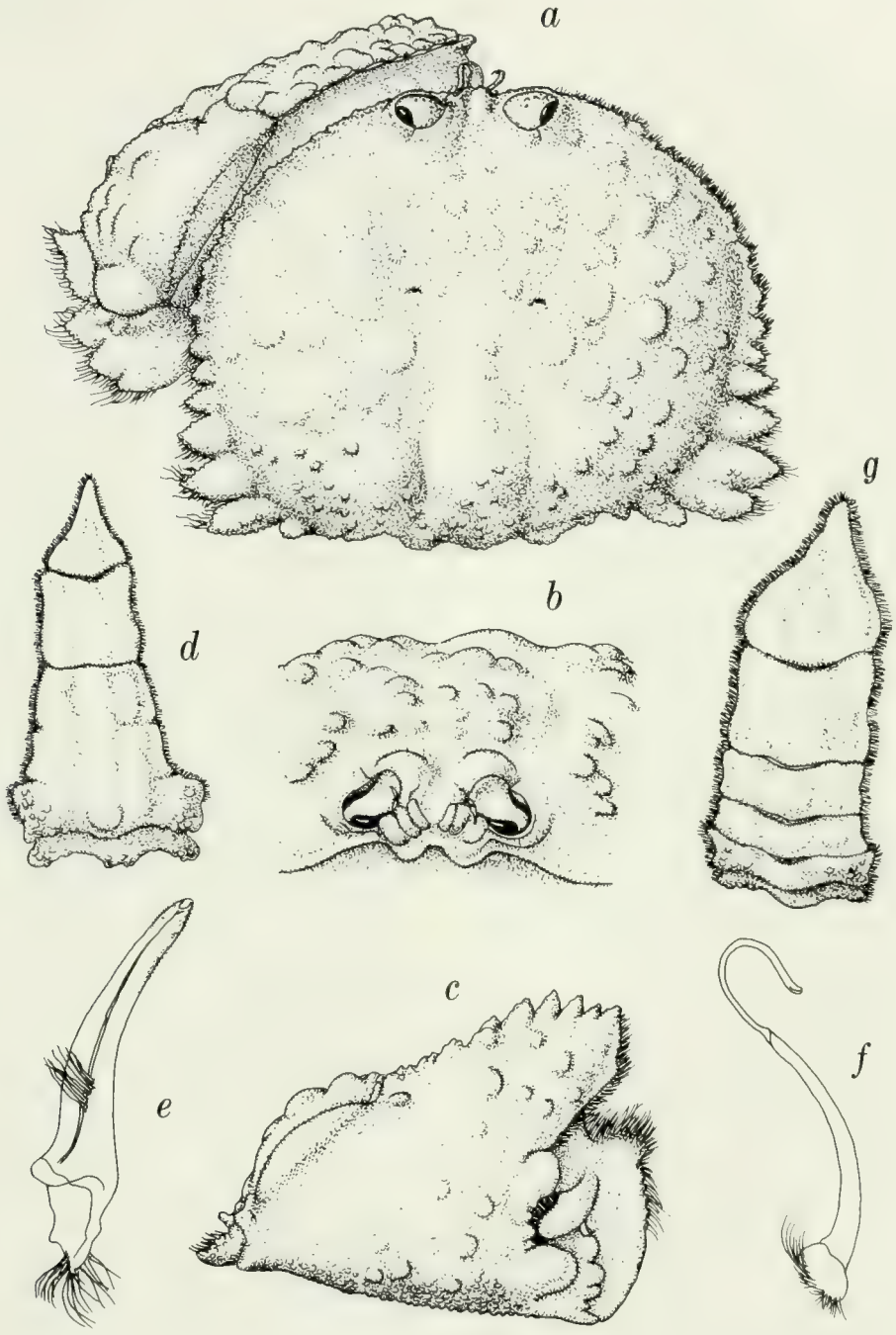

FIGURE 1.—*Calappa tortugae* Rathbun, ♂ holotype, USNM 66382: a, carapace, eyes, and part of left cheliped; b, orbital region in frontal view; c, right chela and part of carpus; d, abdomen; e–f, first and second pleopods. ♀, USNM 202747: g, abdomen.

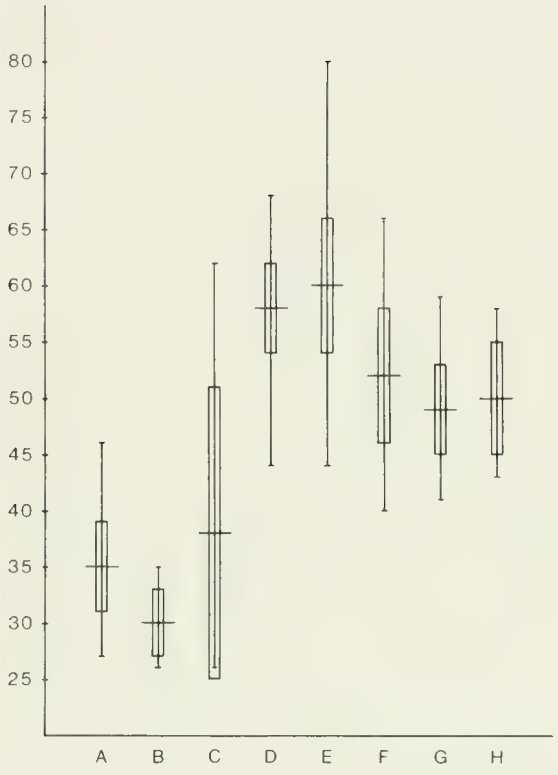

FIGURE 2.—Interorbital width expressed as percent maximum span across posterolateral projections for samples of six species of Calappidae: vertical lines = ranges of percentage; horizontal lines = means; open rectangles = standard deviations. A - *Calappa tortugae*, B - *Calappa saussurei*, juveniles in sample excluded; C - *C. saussurei*, juveniles in sample included; D - *Cyclozodion angustum*, juveniles in type series excluded; E - same, juveniles in type series included; F - *C. tuberatum*; G - *Paracylois atlantis*; H - *P. milneedwardsii*.

stn. 2263. 1 ♀; off St. Augustine, 29°40′N, 80°14′W, 64–87 m; dredge, 7 Oct. 1962.—3438. 1 ♂; off Ormond Beach, 29°34′N, 80°15′W, 73–74 m; dredge, 24 Sept. 1961.—3171. 3 ♂, 2 ♀ (ovig.); same, 29° 30′N, 80°15′W, 71–73 m; dredge, 10 May 1961.—3519. 3 ♂, 4 ♀; Straits of Florida, 24°59′N, 80°14′W, 183 m; dredge, 9 Nov. 1961.—2362. 2 ♂, 1 ♀; off Key Largo, 24°56′N, 80°22′W, 84 m; dredge, 25 Oct. 1960.—2416. 1 ♀; Straits of Florida, 24°18′N, 81°29′W, 229 m; dredge, 28 Oct. 1960.—50. 1 ♀; S of Apalachicola Bay, 28°58′N, 85°20′W, 70–80 m; dredge, 15 July 1957.

Caribbean: *Oregon* stn.—6715. 1 ♂; W Anguilla I., 18°36′N, 63°27′W, 201–238 m; dredge 30 May 1967.—4400. 1 ♀; Venezuela, off Los Mongos Is., 12°37′N, 70°45′W, 97 m; dredge, 26 Sept. 1963.—5036. 1 ♂; Venezuela, off Peninsula de Paria, 11°36′N, 62°54′W, 183 m; dredge, 24 Sept. 1964.

MCZ 6654. 1 juv.; off Sombrero [Is.], 99 m; labeled as *Calappa angusta* A.M.E. paratype.

Diagnosis.—Carapace convex longitudinally and from side to side; mean length 0.9 times mean width (N = 66); surface elevated in median tract and branchial regions, separated by well-marked furrow at each side running from orbit to level of cardiac region but thereafter becoming obsolescent; covered by prominent, densely and minutely granular protuberances of varied size more or less symmetrically arranged, with more widely scattered and larger granules between them; arcuate anterolateral margins finely granulate, with larger granules at intervals; winglike extension with teeth largest at posterolateral angle preceded by up to 4 teeth progressively diminishing in size anteriorly, and followed posteriorly by 2 or 3 smaller teeth successively diminishing in size, all with beaded edges; mean maximal span between tips of posterolateral teeth slightly greater (1.02) than mean maximal span between anterolateral margins; axis of largest tooth on winglike protuberance diverging from midsagittal line at angle of 20–25°.

Front trilobed, downturned, slightly broader than orbits; large central lobe with rather narrowly rounded tip barely visible in dorsal view, smaller lateral lobes directed anteriorly to accommodate narrowly oblique folded antennular peduncles; orbits noticeably raised above surrounding surface; interorbital width relatively narrow, its span relative to maximal span between posterolateral winglike extentions rather narrow (see Figures 1 and 2).

Palms of chelipeds with external surface bearing irregular ornamentation moderately reminiscent of that on carapace; a lower zone of closely crowded coarse granules adjacent to beaded ventral margin, larger widely scattered irregular protuberances in central region becoming stronger and more closely arranged near base of dorsal "cockscomb" (crest of teeth), widely spaced irregular granules between these varying from obsolescent to well formed; short obliquely curved ridge rising from proximolateral corner to end anteriorly in subrectangular angle, crest minutely crenulate and in line with subdistal crest of 4 similar, narrowly separated broad teeth on merus.

Abdomen of each sex broadest at segment 3; latter fused with narrower segments 4 and 5 in male, segments in female relatively broader but essentially linear and free; segment 2 somewhat trilobed and bearing sparsely scattered low granules clustered laterally, segment 3 with much lower relief and low

granules clustered laterally; telson subtriangular. Male pleopod 1 rather stout, slightly curved and conically elongate, tapering to narrow distal opening with nearby cluster of minute horny spinules; pleopod 2 with slender stylet divided into 2 parts, gently curved proximal part stronger than distal part curved mesially upon itself as a crook, distal half of crook extending beyond tip of pleopod 1.

Measurements in mm.—Carapace: smallest ♂ length 14.4, maximum anterior width 15.8, maximum width across winglike projections 15.4; largest ♂, same 35.1, 42.3, 44.8; smallest ♀, same 10.7, 11.5, 11.4; largest ♀, same 29.7, 34.5, 35.7.

Known range.—North Carolina to Florida, around Gulf of Mexico, Leeward Islands to off Venezuela, 13–238 m (see Powers 1977 in part).

Remarks.—Milne Edwards's *Calappa angusta* 1880 has been generically misplaced. The next available name for the species is *Calappa saussurei tortugae* Rathbun 1933, raised to full specific rank.

The young of *C. tortugae* have long been regarded as having the greatest carapace width anterior to the winglike posterolateral projections. That is confirmed by measurements of young individuals noted above, but measurement of a series ranging from juvenile to adult indicates that the winglike posterolateral projections quickly become the widest part of the carapace as growth progresses, as is true of *Calappa* in general. Another way of expressing this width is to compare it with the interorbital distance. Interorbital distance expressed as a percent of maximum span across the posterolateral winglike projections is plotted for measured samples in Figure 2A (N = 71, $\bar{x}$ = 0.347, SD = 0.039). The eyes of *C. tortugae* are relatively smaller and the orbits more elevated than are those of species belonging to either *Paracyclois* or *Cyclozodion* new genus, and it is clear that the indicated ratio lies largely beyond that for these species, although it is comparable to that computed for a sample of *C. saussurei* Rathbun 1898 available in the USNM (Fig. 2B, N = 14, $\bar{x}$ = 0.297, SD = 0.030, juveniles excluded). That sample contains a disproportionate number of very small juveniles; therefore it is useful to compute two ratios for that species, one that excludes the juveniles and one that includes them (Fig. 2C, N = 21, $\bar{x}$ = 0.297, SD = 0.131). These two species of *Calappa* are similar enough to be regarded as a geminate pair from either side of the Central American land mass, as implied by Rathbun's descriptions. The chief difference is that *C. saussurei* has a much more coarsely and uniformly tuberculate extensor face on the palms of the chelae than does *C. tortugae*.

Cyclozodion new genus

Diagnosis.—Carapace slightly wider than long and moderately convex; front narrow and trilobate; median lobe rounded and much broader than lateral lobes; without lateral epibranchial spine or tooth; anterolateral margins regularly arcuate and entire or lightly crenulate, broadest span anterior to juncture with posterolateral margin; each posterolateral margin bearing strongly spiniferous winglike projection, width between principal spines on latter less than greatest width of carapace, axis of principal spine on lobe diverging from midsagittal line at angle of about 40°.

Eyes large, peduncles short, robust, closely encased in oval orbits scarcely raised above surrounding area; interorbital distance 0.40–0.70 (0.80 in smallest juveniles) of span between tips of principal spines on posterolateral margin. Antennules folding obliquely; antennae with quadrate basal article not reaching frontal margin, flagellum very short. Outer maxillipeds with ischium longer than broad, longer than distally truncate merus with its anterointernal angle distinctly notched. Pereopods 2–5 spineless.

Type species.—*Cyclozodion angustum* (A. Milne Edwards 1880).

Etymology.—From the Greek "cyclo", round, and "zodion", a small carved figure, for the shape of the carapace. The gender is neuter.

Remarks.—Two small species fit between *Calappa* and *Paracyclois*. These species have the orbital characteristics of *Paracyclois*. They have posterolateral spines that cover a narrower span than do those of *Calappa*, but in general shape they resemble some juveniles of that genus. The two small species could almost be cited as examples of brachyuran neoteny, for they seemingly maintain a juvenile *Calappa*-like carapace facies while attaining sexual maturity. We are faced with the prospect of further splitting the family by introducing a new genus to contain these two species, or broadening the concept of *Paracyclois* to contain them. However, lack of any spines on the pereopods and shape of the proximolateral ridge on the extensor face of the cheliped palms, to point out only two features, clearly set them apart from *Paracyclois*. Rathbun (1937) and others perhaps unconsciously took the alternate route of accommodating them in

what she called *Calappa angusta*, saying that the narrow span across the posterolateral winglike projections of the young of that species broadened with age into a full *Calappa*-like form. Analysis of measurements on a large series of specimens does not support this viewpoint (see Figure 2), and we therefore choose to erect the new genus for reception of these two small species.

Key to species of *Cyclozodion*

1. Carapace smooth to slightly tuberculate; front with central lobe shallowly concave, margin smooth; chelipeds with upper surface of carpus smooth ..... *C. angustum*
   Carapace definitely tuberculate; front with broadly concave central lobe sharply granular near tip and on margins continuous with mesial margin of lateral lobe; chelipeds with upper surface of carpus tuberculate ..... *C. tuberatum*

Cyclozodion angustum (A. Milne Edwards 1880)

Figures 2, 3

Calappa angusta A. Milne Edwards 1880:18 (part).—A. Milne Edwards and Bouvier 1902:123, pl. 24, figs. 5–8; pl. 25, figs. 1–3; p. 125, fixed type locality.—Rathbun 1937:210 (part, selected juveniles).— Williams 1965:154; 1984:273 (part, selected juveniles).

Material studied.—MCZ 6653. Juvenile holotype; off Barbados, 183 m; *Hassler*, 27–30 Dec. 1871.—MCZ 2702. 1 ♂ (juv.) paratype; off Barbados, 188 m; *Blake* stn. 273, 1878–79.—MCZ 2917. 1 juv. paratype; N Yucatan, Mexico, 23°13′N, 89°16′W, 154 m; *Blake* stn. 86, 1877–78.

Florida: USNM 101419. 1 ♀; off Cape Canaveral, 27°30′N, 78°52′W, 421 m; *Combat* stn. 238, 3 Feb. 1957.—*Silver Bay* stn. 2480. 1 ♂, 2 ♀; 26°06′N, 79°10′W, 223–229 m; dredge, 9 Nov. 1960.—2445. 1 ♂ (juv.); Straits of Florida, 24°08′N, 80°08′W, 252 m; dredge, 3 Nov. 1960.—2452. 4 ♂, 4 ♀, 3 ♀ ovig.; same, 23°30′N, 79°04′W, 228–238 m; dredge, 5 Nov. 1960.

Silver Bay stn. 3467. 1 juv.; off Great Bahama Bank, 27°27′N, 79°00′W, 229–274 m; dredge, 25 Oct. 1961.—3502. 1 juv.; S Great Inagua I., 20°54′N, 73°37′W, 137–183 m; dredge, 5 Nov. 1961.—3496. 1 ♀; same, 20°53′N, 73°42′W, 183 m; dredge, 4 Nov. 1961.—5193. 1 ♂, 1 ♀ (ovig.); Puerto Rico, W Mayaguez, 18°16′N, 67°22′W, 274 m; trawl, 18 Oct. 1963.—*Oregon* stn. 2643. 1 juv.; off Virgin Gorda, B.W.I., 18°03′N, 64°27′W, 274–329 m; trawl, 5 Oct. 1959.—6715. 2 ♂, 1 ♀; W Anguilla I., 18°36′N, 63°27′W. 201–238 m; dredge, 30 May 1967.—5015. 2 ♀ (juv.); off Barbados, 13°02′N, 59°34′W, 201–247 m; dredge, 20 Sept. 1964.—USNM 110230. 1 ♀; same, 91–336 m; J. B. Lewis, NR4-2, date unknown.—USNM 110231. 1 juv.; same, NR8-2.—USNM 110232. 1 ♂ (juv.); same, NR12-4.—*Oregon* stn. 4932. 1 ♀; Honduras Banks off Thunder Knoll, 16°06′N, 81°10′W, 165 m; dredge, 9 June 1964.—4928. 1 ♂, 1 ♀ (juvs.); Colombia off Isla Providencia, 14°05′N, 81°21′W, 183 m; dredge, 8 June 1964.—*Oregon II* stn. 10190. 1 ♀; Nicaragua, off Mosquito Coast, 14°42′N, 81°38′W, 141 m; dredge, 19 Nov. 1968.—10515. 1 ♀ (ovig.); Guyana, N New Amsterdam, 07°47′N, 57°12′W, 95 m; trawl, 28 Apr. 1969.

Description.—Carapace convex, slightly more arched in longitudinal than in transverse profile, length 0.94 width; surface densely but smoothly and uniformly covered with closely crowded granules; obsolescent raised tubercles in median longitudinal row on gastric and cardiac regions and in more or less concentric arcs on branchial regions; raised median tract separated from branchial regions by well-defined longitudinal depression at either side extending from protogastric to intestinal region; anterolateral margin regularly convex, minutely granulate; posterolateral margin extended into winglike prolongation bearing 1 large spine preceded by 3 or 4 much smaller spines, and succeeded by a single obsolescent spine and imperceptibly curved sector converging toward obscurely trilobed posterior margin.

Front trilobed, broader than orbits; broad central lobe concave in dorsal view, downturned, rounded tip not visible; narrower lateral lobes slightly divergent, partly enveloping curved antennular peduncles folded obliquely at slightly less than 45° angle to each other; orbits raised above surrounding region but not markedly so, a single obscure dorsal fissure; mean maximal interorbital distance 0.60 mean maximal span between principal spines on posterolateral winglike extensions.

Chelipeds with ornamentation on extensor surface not well divided into horizontal zones typical of many calappid species; lower margin with almost uniformly crowded obsolescent granules merging into a field of similar granules extending over lower 1/2 of surface; horizontal row of 3–5 low tubercles subparallel to lower margin; 4 or 5 similar scattered tubercles tending to arrangement in diagonal rows in central

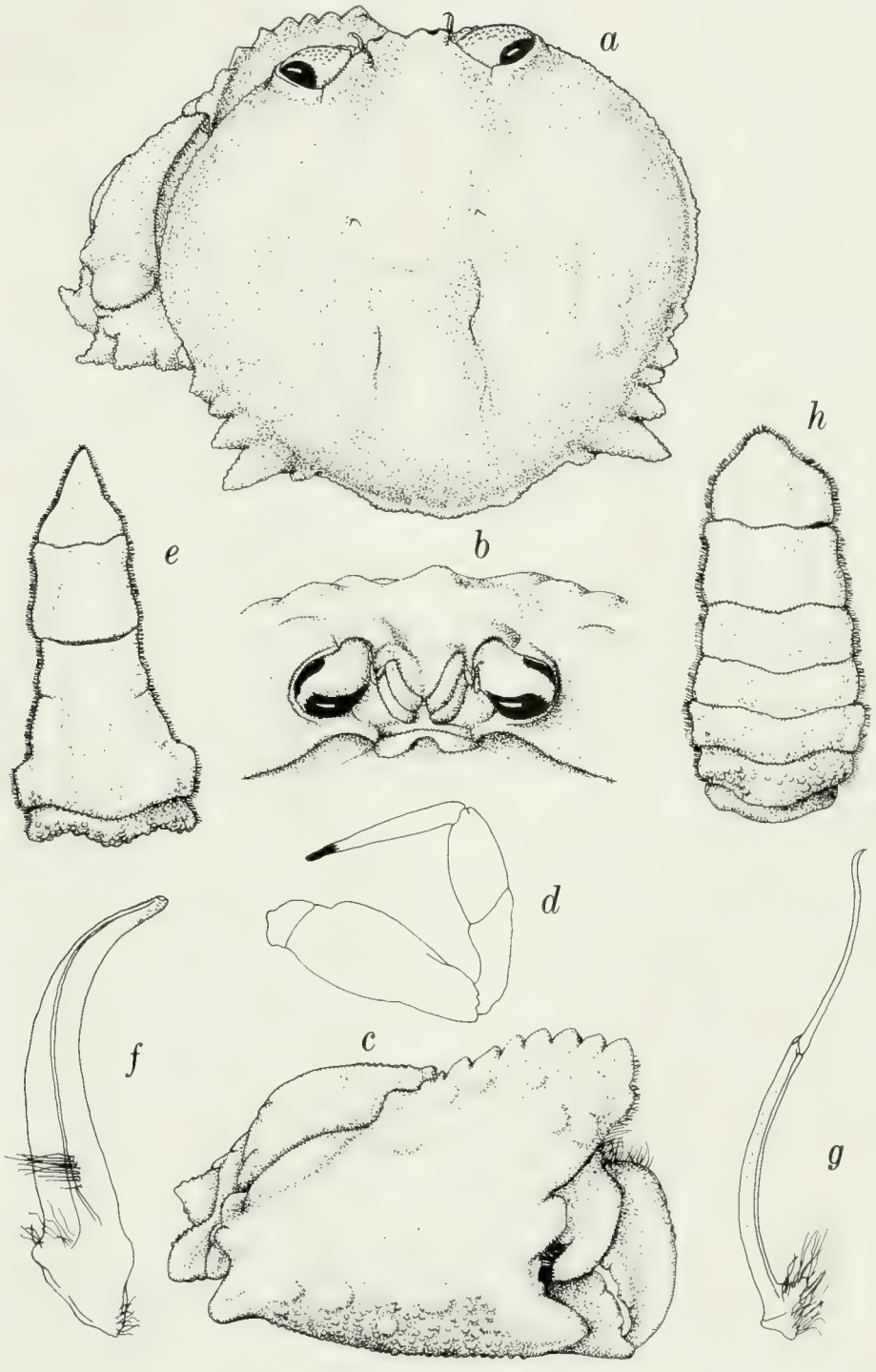

FIGURE 3.—*Cyclozodion angustum* (A. Milne Edwards), ♀ ovigerous, *Silver Bay* stn. 5193: a, carapace, eyes, and part of left cheliped; b, orbital region in frontal view; c, right chela and part of carpus; d, fifth pereopod; h, abdomen. ♂, *Silver Bay* stn. 2452: e, abdomen; f–g, first and second pleopods.

area, and 6–10 more obscure tubercles dorsally near "cockscomb"; a low flattened smooth ridge proximolaterally in line with tubercles subparallel to lower margin and with subdistal crest of broad flattened teeth on merus, anterior tooth of latter with subrectangular tip, second biconcave acute, third and fourth obsolescent and slightly crenulate. Pereopods 2–5 spineless.

Abdomen of each sex broadest at segment 3; latter fused with narrower segments 4 and 5 in male, segments in female relatively broader but essentially linear and free; segment 2 of male somewhat trilobed, that of female less strongly so, each with scattering of obsolescent granules on these members; telson subtriangular. Male pleopod 1 stout, slightly curved and conically elongate, tapering to narrow distal opening with nearby cluster of minute horny spinules; pleopod 2 with slender stylet divided into 2 parts, gently curved proximal part stronger than distal part diverging obliquely mesad, tip only slightly exceeding that of pleopod 1.

Measurements in mm.—Carapace: holotype ♂ length 7.3, maximum anterior width 7.9, maximum span across winglike posterolateral projections 6.5; nontypes, same, smallest ♂ 17.3, 19.0, 15.1; largest ♂ 21.5, 22.9, 18.2; smallest ♀ 19.8, 18.5, 16.1; ovigerous ♀ 26.4, 24.5, 20.8.

Color.—Preserved specimens display a sprinkling of tiny pale orange spots on posterior 2/3 of carapace and upper exposed parts of chelipeds.

Known range.—Florida off Cape Canaveral to Colombia, off Isla Providencia, and Guayana, 95–421 m.

Remarks.—Cyclozodion angustum was originally based on juvenile specimens of quite small size and placed in the genus *Calappa*. Subsequent authors have followed this lead, attributing the narrowed span across the posterolateral winglike projections in all stages from juvenile to adult to youthful allometric phases seen in *Calappa*. Broadening of the winglike span in *C. tortugae* actually becomes established at very early stages, as pointed out above in the discussion of that species.

The eyes are relatively larger than in *C. tortugae*, the orbits less protuberant, and in frontal view the orbits are less elevated above the plane of the beaded anterolateral margin than in that species. Interorbital width expressed as a percent of maximum span across the posterolateral winglike projections is significantly higher in *Cyclozodion angustum* than in *Calappa tortugae*, another indication of the differential in size of orbits and carapace shape in these two species (Fig. 2A, D), although there is minimal overlap in this ratio for a few specimens. Two versions of this ratio are given for *Cyclozodion angustum*: one for the bulk of material measured and analyzed (Fig. 2D, $N = 27$, $\bar{x} = 0.581$, SD = 0.040) and one that includes the very small individuals in the type series (Fig. 2E, $N = 30$, $\bar{x} = 0.595$, SD = 0.060). Except for the range of percentages, indicating the relatively larger eyes of the types, there is no difference between the two sets of data.

Other features that distinguish *C. angustum* and *Calappa tortugae* are found on the chelipeds. The exposed carpal surface is smooth in the former, rough in the latter, and the proximoventral corner of the extensor surface on the palm bears a low rounded crest in the former but an anteriorly subrectangular crest in the latter.

Cyclozodion tuberatum new species

Figures 2, 4

Calappa angusta A. Milne Edwards 1880:18 (part, selected juveniles).—A. Milne Edwards and Bouvier 1902: 123 (part, selected juveniles).

Material studied.—Specimen lots in USNM recorded by Rathbun (1937) under *Calappa angusta* (catalog numbers only) plus material added since that time.

Bahamas: USNM 234462. Holotype ♂; N Little Bahama Bank, 27°55′N, 79°05′W, 183 m; *Silver Bay* stn. 3466, dredge, 25 Oct. 1961.—USNM 234463. Allotype ♀; same.—USNM 234464. Paratype ♂; same, 27°26′N, 78°57′W, 137 m; stn. 3468, dredge, 25 Oct. 1961.—USNM 234465. Paratype ♂; Straits of Florida off Great Bahama Bank, 26°06′N, 79°10′W, 223–229 m; stn. 2480, dredge, 9 Nov. 1960.

North Carolina: USNM 51070.—101676. 1 ♀; off Cape Lookout, 137 m.—*Silver Bay* stn. 3333. 1 ♂; off Cape Fear, 33°48′N, 76°34′W, 73 m; trawl, 14 Aug. 1961.

Florida: USNM 20028, 68505, 68515, 71370, 71371.—169921. 2 unsexed; off Sebastian Inlet, 80 m.—101415. 1 ♂, 1 ♀ (juv.); Florida Straits, 119 m.—77291. 2 ♂; off Key West.—101420. 1 ♀; same, 73–91 m.—101677. 1 ♂; Gulf off W Fla., 31–35 m.—91140. 2 ♂, 1 juv.; same 113 m.

Oregon stn. 6040. 1 ♀; off St. Augustine, 29°47′N, 80°33.5′W, 35 m; dredge, 24 Apr. 1966.—*Silver Bay* stn. 3704. 1 ♀; off Cape Canaveral, 28°30′N,

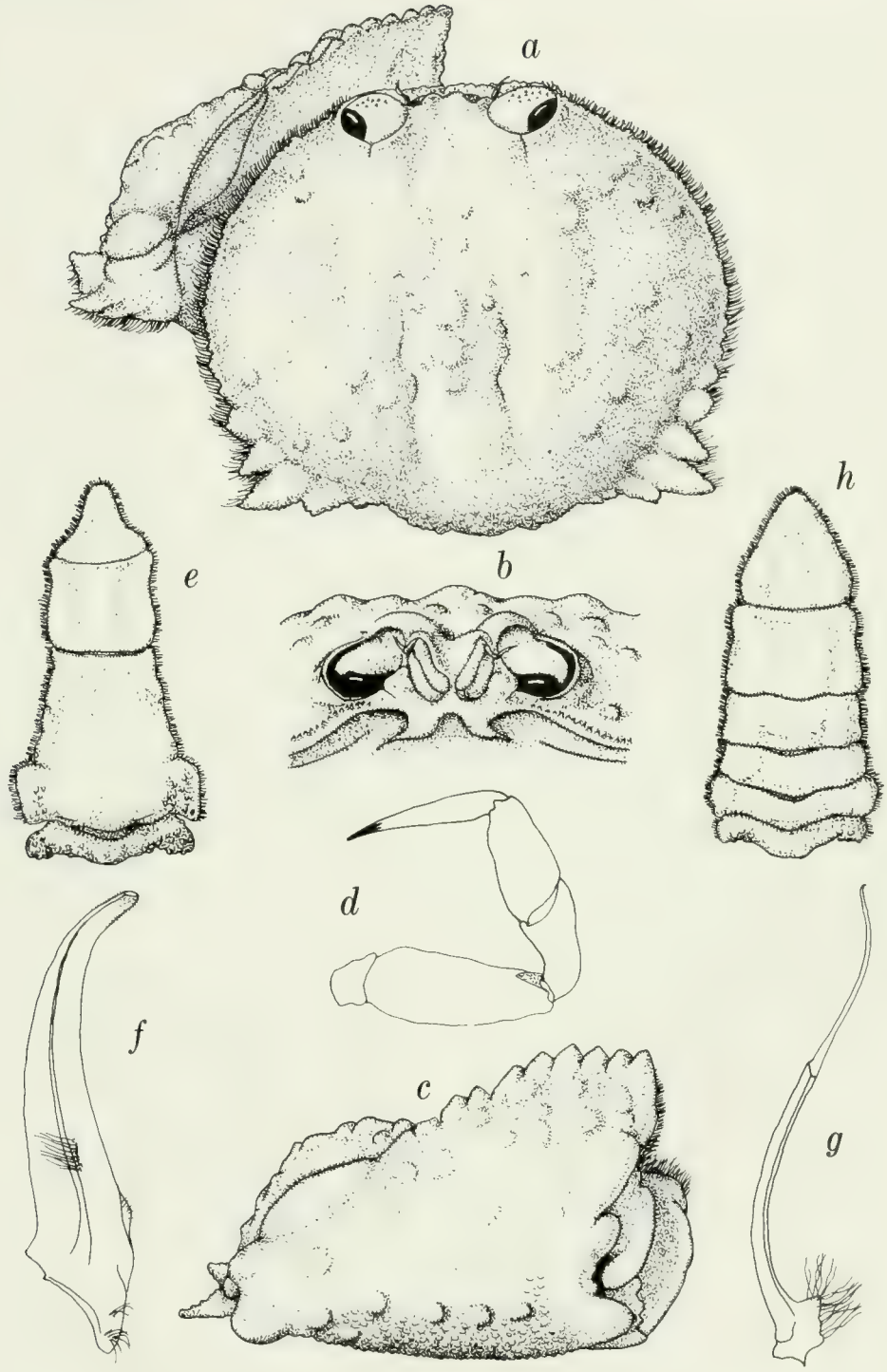

FIGURE 4.—*Cyclozodion tuberatum* new species, ♂ holotype, USNM 234462: a, carapace, eyes, and part of left cheliped; b, orbital region in frontal view; c, right chela and part of carpus; d, fifth pereopod; e, abdomen; f–g, first and second pleopods. ♀ allotype, USNM 234463: h, abdomen.

80°02′W, 68–75 m; dredge, 25 Jan. 1962.—*Triton*. 1 ♂, 1 ♀ (ovig.); off Palm Beach, 183–229 m; Thompson & McGinity, no date.—Same. 1 damaged; off Palm Beach, 55–73 m; 20 Apr. 1950.—Same. 3 juv.; SW Sombrero Lt., 165–183 m; 6 June 1950.—Schmitt stn. 207. 1 ♂; Tortugas, 17.7 km (11 mi) S Loggerhead Key, 68 m; dredge, 10 June 1925.—*Oregon* stn. 4084. 1 ♀; Gulf of Mexico W Tampa, 27°45′N, 84°27′W, 91 m; dredge, 4 Dec. 1962.—*Pelican* stn. 143-2. 1 ♂; SW Panama City, 29°49.5′ N, 86°23′W, 70 m; try net, 5 Mar. 1939.—*Silver Bay* stn. 2455. 1 ♀ (ovig.); S Great Bahama Bank, 23°34′N, 79°03′W, 165–188 m; dredge, 5 Nov. 1960.—3502. 1 ♂, 1 ♀; S Great Inagua I., 20°54′N, 73°37′W, 137–183 m; dredge, 5 Nov. 1961.—*Oregon* stn. 4297. 1 ♀; Surinam off Nieuw Amsterdam, 07°46′N, 54°17′W, 640 m; trawl, 22 Mar. 1963.

Description.—Carapace convex, slightly more arched in longitudinal than in transverse profile, length 0.92 width; low tubercles of varied sizes scattered more or less symmetrically, much bolder on gastric, cardiac, and anterior branchial regions than on posterior 1/3 and tract within perimeter, similar raised ornamentation on extensor surfaces of chelipeds; tubercles covered with low, smooth, tightly packed granules, but surface between elevations more coarsely and less thickly granular; raised median tract on gastric and cardiac region separated from branchial regions by well-defined but shallow depression to either side extending from postorbital to intestinal regions; anterolateral margins regularly convex, rather evenly and closely granular but 2 or 3 remote slightly larger granules along hepatic margins and tendency to development of broad obsolescent teeth near juncture with posterolateral margin; posterolateral margin extended into winglike prolongation bearing large spine preceded by 3 or 4 much smaller and increasingly diminished spines, and succeeded by small spine, a rudimentary tubercle, and flared arch over coxa of pereopod 5; posterior margin obscurely trilobed, lateral lobes extended ventrally to flank base of abdomen, intestinal region adjacent to median lobe coarsely granulate. Front trilobed, broader than orbit; central lobe broadly concave, downturned, narrowly rounded tip not visible in dorsal view, sharply granular near tip and on raised margins continuous with mesial margin of lateral lobes, latter directed almost straight forward; slightly curved basal article of antennular peduncles folded at less than 45° to each other. Orbits raised above surrounding region; a single obscure dorsal suture; mean maximal interorbital distance 0.52 mean maximal span between principal spines on posterolateral winglike extensions.

Palm of chelipeds with ornamentation on extensor surface not well divided into horizontal zones typical of calappid species; lower margin with almost uniformly crowded, well-formed granules merging into a horizontal field of similar granules extending over lower part of palm and bounded by almost horizontal row of 5 or 6 low tubercles; surface above this covered thickly with obsolescent granules and a scattering of widely spaced low tubercles of varied sizes tending to diagonal arrangement, crowded more closely at base of "cockscomb"; a low, flattened, smoothly arched ridge, obliquely situated and sometimes dorsally cupped, at posterolateral corner in line with flattened subdistal crest on merus, latter divided into anterior rectangulo-acute tooth, followed by a biconcave tooth and 2 more lower teeth, all slightly crenulate on margins; field above this crest coarsely granulate; exposed surface of carpus tuberculate and granulate like palm.

Abdomen of each sex broadest at segment 3; latter fused with narrower segments 4 and 5 in male, segments in female relatively broader but essentially linear and free; segment 2 somewhat trilobed and bearing scattered obsolescent granules, segment 3 with much lower relief and low granules scattered laterally; telson subtriangular. Pleopod 1 stout, slightly curved and conically elongate, tapering to narrow distal opening with nearby cluster of minute horny spinules; pleopod 2 with slender stylet divided into 2 parts, gently curved proximal part stronger than distal part diverging obliquely mesad, tip only slightly exceeding that of pleopod 1.

Measurements in mm.—Carapace: holotype ♂ length 20.6, maximum anterior width 23.2, maximum span across winglike posterolateral projections 20.7; nontypes, same, smallest ♂ 16.0, 16.1, 14.9; smallest ♀ 12.0, 12.6, 10.9; allotype ♀ 21.1, 23.1, 21.7.

Color.—No evidence of persistent minute spots of color as on preserved specimens of *Calappa angusta*.

Known range.—North Carolina off Cape Lookout through Bahamas, eastern Gulf of Mexico, Surinam; 31–188, rarely 640 m.

Etymology.—The name is from the Latin "tuberatus", covered with knobs or bosses.

Remarks.—*Cyclozodion tuberatum* has been confused with *Calappa tortugae* because of the similar-

ity in ornamentation. However, body proportions of the two species differ, as exemplified by the relationship of interorbital width to maximum span between posterolateral projections of the carapace (Fig. 2A, F, $N = 40$, $\bar{x} = 0.519$, SD = 0.057). Other differences include shape of the proximoventral crest on the extensor face of the cheliped palm, rounded in the former, ending anteriorly in a subrectangular point in the latter, and in shape of the male pleopod 1 (see Figures 1 and 4). *Cyclozodion tuberatum* most closely resembles *Calappa angustum*, although there are superficial similarities to fossil *Calappilia scopuli* Quayle and Collins as pointed out below.

Paracyclois Miers 1886

Paracyclois Miers 1886:288. Type species, *P. milneedwardsii* Miers 1886:288.—Glaessner 1969:R494 (part, not *Calappilia*).

Diagnosis paraphrased and emended.—Carapace about as long as broad, and moderately convex; front narrow and trilobate; median lobe rounded and much broader than lateral lobes; without lateral epibranchial spine or tooth; anterolateral margins regularly arcuate, broadest span anterior to juncture with posterolateral margin; each posterolateral margin bearing strongly spiniferous lobe or winglike projection, width between principal spines on lobes less than greatest width of carapace (posterolateral winglike prolongations more fully developed in *Calappa*); axis of principal spine on winglike projection diverging from midsagittal line at angle of 25–40°. Subhepatic regions of carapace concave; channel thus formed communicating with antennary region (and thereby with buccal cavity) by a notch situated between it and inferior wall of orbit. Posterior abdominal segments distinct.

Eyes large, peduncles short, robust, closely encased in oval orbits scarcely raised above surrounding area; interorbital distance at least 0.40 and usually 0.45–0.60 or more of span between tips of principal spines on posterolateral margin. Antennules folding obliquely; antennae with quadrate basal article not reaching frontal margin, flagellum very short. Outer maxillipeds with ischium longer than broad, longer than distally truncate merus with its anterointernal angle distinctly notched. Pereopods 2–5 with row of spines on flexor surface of ischium-merus.

Remarks.—Miers (1886, emended) considered *Paracyclois* to be an apparent connecting link between *Calappa*, *Cycloes* De Haan 1837, and *Platymera* H. Milne Edwards 1837 in which the merus of the outer maxilliped is distally truncate and bears the next article at its anterointernal angle, which is prolonged in the form of a lobe or tooth; but *Paracyclois* is distinguished from the first two of the above-mentioned genera by the absence of any lateral spine on the margin of the carapace and the broader basal antennal article, and from *Calappa* by both the reduced winglike prolongations of the carapace which bear strong spines, and by presence of spines on the flexor margin of the ischium and merus of pereopods 2–5.

Key to species of *Paracyclois*

1. Carapace with 3 obviously projecting lobulate spines on posterior margin ..... *P. milneedwardsii*
   Carapace with posterior margin only faintly trilobed ..... *P. atlantis*

Paracyclois atlantis Chace 1939

Figures 2, 5

Paracyclois atlantis Chace 1939:51.—1940:27, figs. 11, 12.

Material studied.—*Silver Bay* stn.—3467. 1 ♂; off Grand Bahama Bank, 27°27′N, 79°00′W, 228–274 m; dredge, 25 Oct. 1961.—3510. 2 ♂; Santaren Channel, 22°55′N, 78°36′W, 273 m; dredge, 7 Nov. 1961.—USNM 81986. 1 ♀; off Punta Alegre, Cuba, 22°46.5′N, 79°W, 329 m; *Atlantis* stn. 3419, 30 Apr. 1939.—*Oregon* stn. 2603. 3 ♂, 1 ♀ (ovig.); Puerto Rico, E San Juan, 18°30′N, 65°55′W, 256–292 m; trawl, 25 Sept. 1959.—5914. 1 ♂, 2 ♀, Leeward Is., W Anguilla I., 18°13′N, 63°19′W, 201 m; dredge, 25 Feb. 1966.—6700. 3 ♂; S Barbuda I., 17°27′N, 62°04′W, 248–285 m; trawl, 19 May 1967.—3636. 1 ♂; Belize, 17°17′N, 87°59′W, 228 m; trawl, 10 June 1962.—4445. 1 juv.; Netherlands Antilles, S Bonaire, 10°50′N, 68°00′W, 183 m; trawl, 10 Oct. 1963.—4856. 1 ♀; Colombia, off Barranquilla Is., 11°08′N, 74°23.8′W, 183 m; trawl, 19 May 1964.—*Oregon* stn. 3585. 1 ♂; Panama, Gulf of Mosquitos, 09°12′N, 81°30′W, 247–256 m; trawl, 25 May 1962.—3587. 1 ♂; Panama, Canal Zone, 09°18′N, 80°25′W, 137 m; trawl, 29 May 1962.—1983. 1 ♀; Venezuela off Orinoco R. mouths, 09°53′N, 59°53′W, 228 m; trawl, 3 Nov. 1957.—2294. 1 ♀; Surinam E of Paramaribo, 07°25′N, 54°08′W, 192–210 m; trawl, 9 Sept. 1958.

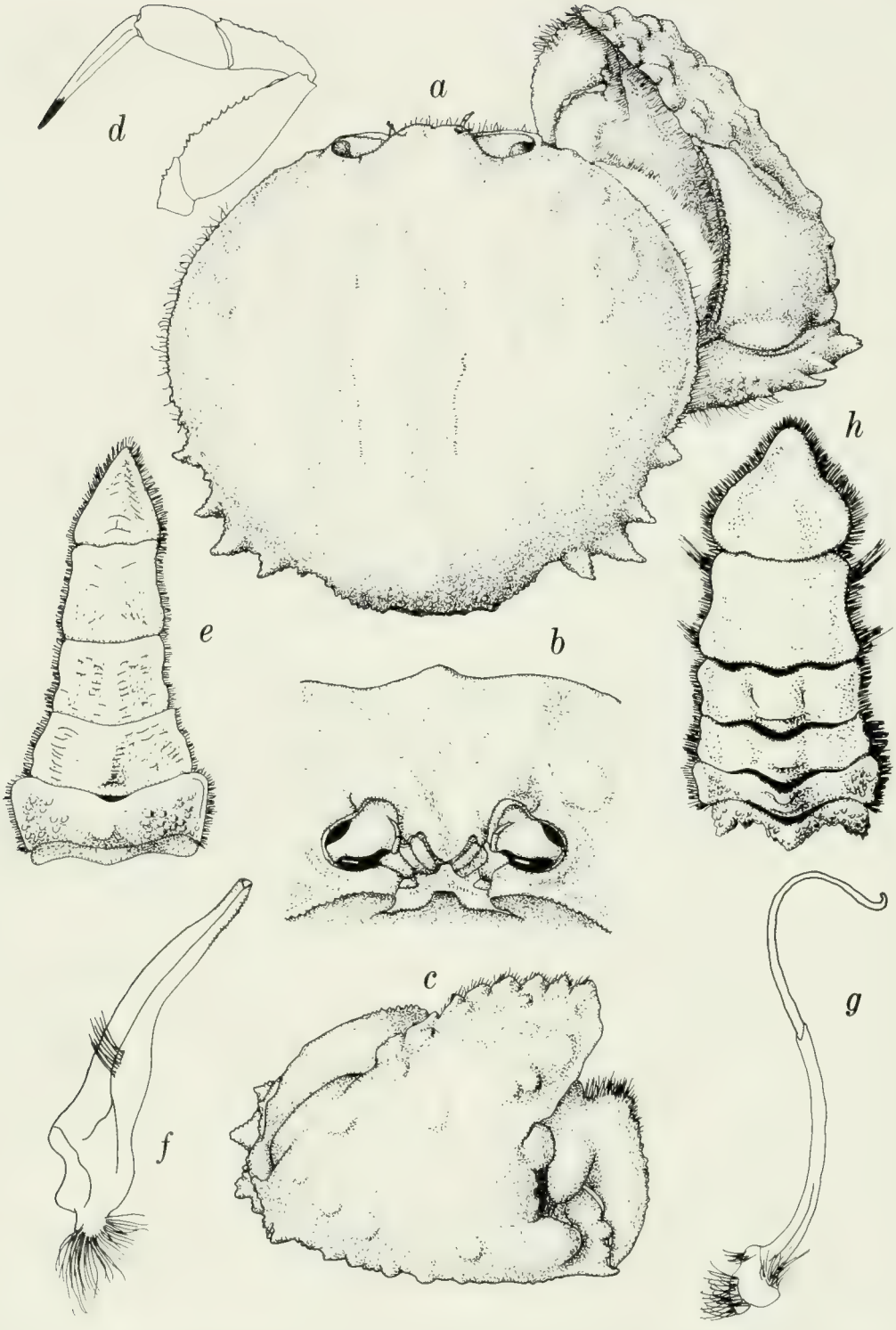

FIGURE 5.—*Paracyclois atlantis* Chace, ♂ *Silver Bay* stn. 3510: a, carapace, eyes, and part of right cheliped; b, orbital region in frontal view; c, right chela and part of carpus; d, fifth pereopod; e, abdomen; f–g, first and second pleopods. ♀, Oregon stn. 5914: h, abdomen.

Diagnosis.—Carapace convex longitudinally and from side to side except where posterolateral winglike extensions occur; surface uneven, elevations roughly falling into 5 longitudinal rows, pair of furrows bordering median elevation deepest by far; minutely granular and coarsely punctate except on extreme posterior part where punctations disappear and granules become larger; small posterolateral winglike projections bearing 4 large and 1 or 2 rudimentary spines, 1 rudimentary spine often present between 2 anterior larger ones, spine next to posteriormost always largest and very much so in juveniles, somewhat curved anteriorly, with tendency for anterior curvature in others as well; posterior margin trilobate in dorsal view, lateral lobes prolonged ventrally on either side of abdomen.

Front deflexed, tip invisible in dorsal view, very slightly wider than greatest diameter of orbit and trilobate, median lobe rounded triangular and lateral lobes very narrow and traversed by notch separating front from orbits; orbital margin very slightly raised above surrounding region; mean maximal interorbital distance 0.50 mean maximal span between major posterolateral spines (see Figure 2G).

Palm of chelipeds with extensor surface ornamented in horizontal zones, well defined in lower 1/4 but obscure in upper 3/4; lower margin beaded with sharp granules, progressively raised, spiniform and remote proximally, flanked by narrow band of moderately crowded granules; lower half bearing low scattered protuberances, partly interspersed in granular zone and tending to horizontal arrangement, but becoming more widely and somewhat diagonally scattered in upper 1/2; proximolateral corner bearing short oblique obsolescent ridge surmounted by 3 or more acute to crenulate spines, most prominent distally; in line with subdistal crest of larger, uneven, ragged spines on merus. Pereopods 2–5 with row of almost uniform spines on flexor surface of merus, extensor surface of carpus entire.

Abdomen of each sex broadest at segment 3, latter fused with narrower segments 4 and 5 in male though nonfunctional articulations sometimes apparent, segments in female relatively broader but essentially linear and free; segment 2 trilobed and rather sharply granular, segment 3 with lower relief and bearing obsolescent granules clustered laterally; telson subtriangular. Male pleopod 1 rather stout, slightly curved and conically elongate, tapering to distal opening; pleopod 2 with slender stylet divided into 2 parts, gently curved proximal part stronger than distal part curved mesially upon itself as a crook, distal half of crook extending beyond tip of pleopod 1 and recurved near tip.

Known range.—Grand Bahama Bank to Panama and Surinam, 137–365 m.

Measurements in mm.—Carapace: smallest ♂ length 19.8, maximum anterior width 20.7, maximum span across posterolateral winglike projections 17.2; same, largest ♂, 57.1, 62.2, 50.5; smallest ♀, 20.6, 22.2, 18.3; largest ♀, 53.2, 58.5, 48.7.

Remarks.—See next species.

***Paracyclois milneedwardsii* Miers 1886**

Figures 2, 6

Paracyclois milneedwardsii Miers 1886:289, pl. 24, fig. 1.—Sakai 1976:134 (Engl. text), 85 (Jpn. text), pl. 41, fig. 2.
Calappilia milne-edwardsi.—Glaessner 1969:R494.

Material studied.—USNM 233655. 2 ♂, 2 ♀; Japan, Shikoku I., Tosa Bay; K. Sakai.—233654. 1 ♀; Philippines, Balayan Bay, southern Luzon, 13° 47′20″N, 120°43′30″E, 329 m; *Albatross* stn. 536, trawl, 20 Feb. 1909.—Same. 1 ♀; S Balayan Town, 141–195 m; trawl, 21 June 1966.—Same. 1♂; S Sapating, 270–305 m; trawl, 29 July 1966.—*Albatross* stn. 5453. 2 ♀; E coast Luzon, San Bernardino Str., NE Legaspi Light, 13°12′N, 123°49′18″E, 267 m; trawl, 7 June 1909.—5242. 2 ♂ (juv.). Mindanao near Vanivan Is., 06°51′53″N, 126°14′10″E, 349 m; trawl, 14 May 1908.

Diagnosis.—Carapace irregularly orbiculate, broadest at a point anterior to midlength of anterolateral margins, latter sweeping in regular curve to winglike protuberance of posterolateral margins bearing 4 unequal spines, anterior one longest; posterior margin bearing 3 strong flattened lobular spines ornamented with coarse tubercles extending onto adjacent intestinal region; margins behind anterior 1/4 of length tending to be rimmed by narrowly upturned, granular lip; median tract separated from branchial regions by rather prominent groove at either side extending from gastric to intestinal regions; surface granular and ornamented with low, smooth rounded tubercles tending to arrangement in concentric arcs diminishing in size toward lateral, posterolateral, and intestinal areas.

Front slightly narrower than orbit, trilobed, broadly rounded central lobe with downturned tip not visible in dorsal view, 3 low peripheral lobes on its upper surface; lateral lobes much narrower and slightly divergent to accommodate folded anten-

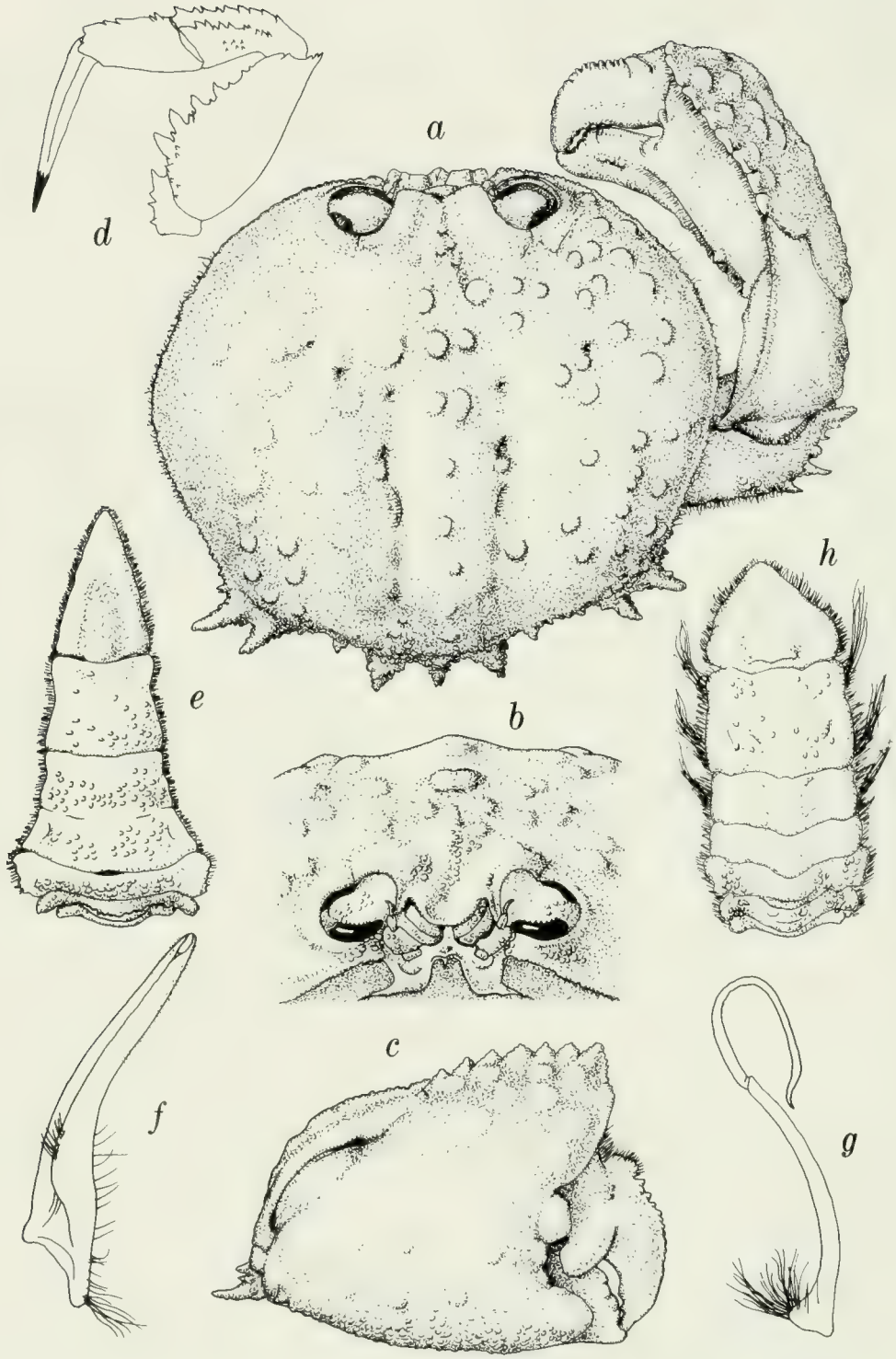

FIGURE 6.—*Paracyclois milneedwardsii* Miers, ♂, USNM 233655: a, carapace, eyes, and part of right cheliped; b, orbital region in frontal view, c, right chela and part of carpus; d, fifth pereopod, e, abdomen; f–g, first and second pleopods. ♀, USNM 233654: h, abdomen.

nular peduncles; ocular peduncles short and thick, granulated above; orbital margins slightly raised above surrounding region, mean maximal interorbital distance 0.50 mean maximal span between major posterolateral spines (Fig. 2H, $N = 7$, SD = 0.051).

Palm of chelipeds with ornamentation on extensor surface obscurely arranged in horizontal zones; lower margin granulate, sharply so in proximal 3/4; lower 1/3 of surface coarsely granular, becoming less sharply so as it merges into central zone; upper 2/3 bearing obscure diagonal rows of obsolescent tubercles in central portion, but stronger and less regularly arranged tubercles near base of dorsal "cockscomb"; a spine near proximoventral corner in line with subdistal row of ragged, forward trending spines on merus. Pereopods with flexor surface of ischium and merus strongly but irregularly spinose; carpus bearing biserial row of smaller spines on extensor surface.

Abdomen of each sex broadest at segment 3; latter fused with narrower segments 4 and 5 in male, segments in female relatively broader but essentially linear and free; segment 2 trilobed, less so in female than in male and bearing obsolescent granules closely clustered or fused on lobes, segment 3 with much lower relief and obsolescent granules clustered mainly on lobes; telson subtriangular. Male pleopod 1 rather stout, slightly curved and conically elongate, tapering to narrow distal opening; pleopod 2 with slender stylet divided into 2 parts, gently curved proximal part stronger than distal part curved mesially upon itself as a rather closed crook, distal half of crook extending beyond tip of pleopod and recurved near tip.

Known range.—Japan, Philippines, the type locality north of Admiralty Islands (Sakai 1976), 141–349 m for specimens studied.

Measurements in mm.—Carapace: smallest ♂ length 18.2, maximum anterior width 17.3, maximum span across posterolateral winglike projections 15.4; same, largest ♂, 53.2, 53.3, 47.8; smallest ♀, 21.3, 19.9, 17.7; largest ♀, 45.6, 44.8, 40.4.

Remarks.—The two species of *Paracyclois*, basically similar in carapace outline, have relatively larger eyes and orbits than the two species of *Calappa* discussed above (Fig. 2), and the orbits in frontal view are less elevated above the plane of the anterolateral margin. Interorbital width expressed as percent of maximum span across the posterolateral projections is virtually the same in samples of the two species (*P. atlantis*, $N = 20$, $\bar{x} = 0.494$, SD = 0.044, Fig. 2G; *P. milneedwardsii*, $N = 10$, $\bar{x} = 0.496$, SD = 0.051, Fig. 2H). Spination of the posterolateral projections is much more slender and remote than in either *Calappa* or *Cyclozodion*, and well-developed spination on the chelipeds and ventral margin of the ischium-merus of the fifth legs clearly sets them apart from species of these genera. Distribution in two well-separated centers, western Indo-Pacific and Caribbean, seems to reflect an ancient Tethyan track.

Calappilia A. Milne Edwards 1873

Calappilia A. Milne Edwards 1873:434.—Rathbun 1930:7.—Glaessner 1969:R494 (part, not *Paracyclois*).

Ross and Scolaro (1964) summarized scattered references to fossil species of *Calappilia* known up to that time, Glaessner (1929) compiled a listing and an overview (1969), and Quayle and Collins (1981) gave notes along with description of an additional species. We reviewed all references to these species, and examined selected species (*) in the paleontological crustacean collection of the USNM in order to compare features of *Calappilia* with those of other genera treated herein.

Five species of *Calappilia* are known from the western hemisphere: **C. hondoensis* Rathbun 1930, Upper Eocene, Calif.; *C. bonairensis* Van Straelen 1933, Upper Eocene, Bonaire, Netherlands, West Indies; **C. diglypta* Stenzel 1934, Middle Eocene, Tex.; *C.* sp.? Roberts 1956, Lower Eocene, N.J.; **C. brooksi* Ross and Scolaro 1964, Upper Eocene, Fla.

Seven species and one variety are known from Europe: *C. verrucosa* A. Milne Edwards 1873, the type species, and *C. sexdentata* A. Milne Edwards 1876, Middle Oligocene, SW France; *C. perlata* Noelting 1885, Lower Oligocene, Germany; *C. incisa* Bittner 1886, Middle Eocene, Italy; *C. dacica* Bittner 1886, Middle-Upper Eocene, Hungary; *C. dacica* var. *lyrata* Lörenthy and Beurlen 1929, Upper Eocene, Hungary; *C. vicetina* Fabiani 1910, Upper Eocene, Italy; *C. scopuli* Quayle and Collins 1981, Upper Eocene, England.

Two species are known from the East Indies: *C. borneoensis* Van Straelen 1923, Middle Eocene, Borneo; *C. bohmi* Glaessner 1929, Upper Eocene, Java.

Diagnosis.—For purposes of comparing *Calappilia* with *Calappa*, *Cyclozodion*, and *Paracyclois*,

we paraphrase essential features of A. Milne Edwards's original description.

Near *Calappa* and *Mursia*; distinguished from former because carapace not extended above ambulatory legs (Fig. 7) in manner of a shield, and from latter by absence of large spines laterally prolonged beyond cephalothoracic shield; front very narrow and ornamented with 2 small slightly divergent points very similar to those of *Calappa*; [orbital] border cut by two narrow fissures.

FIGURE 7.—*Calappilia brooksi* Ross and Scolaro, carapace and left eyestalk; USNM 648599, Upper Eocene, Fla.

Carapace very convex, recalling that of *Calappa* or certain representative Leucosiidae; gastric and cardiac regions separated in lateral portions by deep grooves; hepatic region not clearly delimited; branchial region very inflated in anterior part but much narrowed posteriorly, surface covered with coarse tubercles in anterior part; posterior branchial lobe extended, constituting a prominence directed laterally and a little posteriorly; posterior border bearing a tubercle much less developed than branchial prominence at level of branchiocardiac groove.

Ambulatory legs missing; fragment of chela with very compressed dactyl bearing granular crest, armed at base with large tubercle recalling that developed in *Calappa*; palm covered with large tubercles analogous to those ornamenting carapace, and their size notable compared to those on body.

Measurements of selected species in mm.—Carapace: *C. brooksi* length 18.8, width 21.5; *C. dacica* length 32, width 37; *C. hondoensis* length 19, width 18.7.

Remarks.— The features of *Calappilia* mentioned by A. Milne Edwards suggest much closer similarity to *Calappa* than to *Paracyclois*, and the brief diagnosis by Rathbun (1930) confirms this in broad outline. All of the species of *Calappilia* are small, comparing favorably with the range of sizes shown by the two species of *Cyclozodion* described here. There is considerable diversity in ornamentation of the carapace among species of *Calappilia*, with a tendency to development of coarse tubercules dorsally and along the margins, especially posterolaterally, but minimal development of posterolateral winglike projections, with some exceptions. Lobular tubercles along this margin are usually similar in size, although in *C. scopuli* (Quayle and Collins 1981:740, pl. 104, fig. 8) there is a developed posterolateral spine and, except for the problematic frontoorbital region, a marked similarity to *Cyclozodion* in outline of the carapace. The holotype of *Calappilia hondoensis* (USNM 371094) has an obscure posterolateral spine rather wider than long. Rathbun (1930) pointed out that Milne Edwards's (1873) figure of *C. verrucosa* is longer than wide whereas the measurements given show it wider than long. The left eyestalk of *C. brooksi* (USNM 648599, Fig. 7), fossilized projecting forward in its orbit, seems relatively slender compared with eyestalks of both *Cyclozodion* and *Paracyclois*, although only a remnant of it may be preserved.

On the basis of size, shape, and ornamentation of the carapace, relative thickness of eyestalks, and age, we regard Early Tertiary *Calappilia* and Recent *Paracyclois* as distinct. *Calappilia scopuli* and perhaps *C. hondoensis* seem to form closer links with Recent *Cyclozodion* than with *Calappa*, emphasizing similarities among the latter three genera.

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YELLOWFIN TUNA, *THUNNUS ALBACARES*, CATCH RATES IN THE WESTERN PACIFIC

TOM POLACHECK[1]

ABSTRACT

The surface fishery for yellowfin tuna, *Thunnus albacares*, in the western Pacific has increased dramatically since 1978. Catch and effort statistics from the Japanese purse seine and longline fisheries are examined in terms of changes in catch rates and the interaction between these two fisheries. In spite of a 10-fold increase in surface catches to around 100,000 metric tons per year, purse seine catch rates have remained relatively constant. Longline catch rates since 1980 have been declining, with the exception of high rates in 1983. Comparison of purse seine and longline catch rates within the same area and time period indicated no relation between them and suggests that the yellowfin tuna stocks are not homogeneous with respect to the two gears. In addition, observed changes in longline catch rates within areas of the western Pacific appear not to be related to the magnitude of the purse seine catches within these areas. The results provide no direct evidence for any interactions between the two gears, but whether purse seine catches are contributing to the possible, overall decline in longline catch rates remains an open question.

Purse seine catches of yellowfin tuna, *Thunnus albacares*, in the western Pacific have increased from 8,000 to 10,000 t (metric tons) in 1978 (Habib 1984[2]) to estimates of around 100,000 t in 1984. Prior to the advent of purse seining, the main vessels harvesting yellowfin tuna in this region were the Japanese, Korean, and Taiwanese longliners. Longliners still continue to harvest significant amounts of yellowfin tuna (an estimated 60,000 t in 1984). The effect of this 10-fold increase in purse seine catches since 1978, both on the overall stocks of yellowfin tuna in the western Pacific and the effect of the purse seine catches on the longline fisheries, is unknown, but the status of yellowfin tuna stocks is a critical question for a number of reasons. Yellowfin tuna represent the second largest fishery resource for the tropical western Pacific area. Yet, there is no adequate assessment of the magnitude of the harvestable catch for the region, while yellowfin tuna stocks in other regions appear vulnerable to overexploitation by purse seiners (IATTC 1979, 1980, 1981, 1982; Fonteneau and Diouf 1983; Au 1983). In addition, about two-thirds of the yellowfin tuna longline catch is targeted for the Japanese sashimi market and, as such, has an economic value exceeding that of the purse seine-caught fish. Longliners harvest older and larger fish than purse seiners (Cole 1980). In the present paper, the most recent data available on the catch and effort for yellowfin tuna are examined for information on the current yellowfin tuna stocks and on the interaction between longline and purse seine fisheries.

METHODS

Data

The data available for examining catch rates come from records of daily catch and effort supplied by vessels to individual island states in the western Pacific as part of access arrangements which allow vessels to fish within the 200-mile EEZ's (Exclusive Economic Zone) of these states. These catch records have been subsequently transmitted to the Tuna and Billfish Assessment Programme of the South Pacific Commission (SPC), and have formed the core of the regional statistical data base. Data are only supplied as a requirement of access for fishing within EEZ's. While some vessels include activity in international waters in their reports, the available data are relatively incomplete for these waters. Also, for some states in past years, adequate data reporting was not included in the access agreements. In addition, prior to 1984 almost no data are available from United States and some other eastern Pacific purse seiners.

Because of incompleteness and limitations in the

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[2]Habib, G. 1984. An overview of the purpose seine tuna fishery in the central/western Pacific and development opportunities for island states. Workshop on National Fishing Operations, Tarawa, Kiribati, 28 May–4 June 1984.

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available data, the analyses in this present paper are based on catch rates for Japanese vessels. These data form the most extensive and complete set of data currently available to the SPC. Records of daily fishing activity go back as far as the second half of 1978 for the longline fishery and 1979 for the purse seine fishery. However, these earliest data are not complete and need to be interpreted with caution.

The stock or subpopulation structure and their geographic limits for yellowfin tuna in the Pacific are unknown despite considerable tagging and genetic research (Cole 1980). However, a single stock spanning the entire Pacific is considered unlikely. For the present paper, the geographic boundaries used for the western Pacific are from long. 130°E to 180°E and from lat. 10°S to 15°N. For the Japanese purse seine fishery, this area encompasses virtually all of the reported catch and effort data. For the Japanese longline fishery, this represents an area in which the fishery has been relatively consistent and its reporting fairly complete.

Catch Rates

Catch rates or catch per unit effort are calculated below as a measure of relative abundance. An extensive literature exists on the use of catch rates as abundance indices (Gulland 1956a; Beverton and Holt 1957; Paloheimo and Dickie 1964; Allen and Punsley 1984). However, the question of the relation between catch rates and abundance for these yellowfin tuna fisheries needs further research (see Discussion).

For longlining, the effort measure used here is the number of hooks set (in thousands). Catch is reported as the number of fish caught. For purse seining, the effort measure used is the number of days in which vessels made a set or were actively searching for schools of tuna. The catch is recorded in metric tons. In the earliest purse seine data, there may be an underestimation of effort, as it is not clear whether days in which vessels were searching for fish, but did not catch any, were accurately reported.

The average catch rates and their variances within any statistical stratum were calculated as the weighted mean of the observed catch rates for all cruises within the stratum. Thus, an individual cruise's catch rate within a stratum constitutes the primary sampling unit or replicate in the analyses below. The weights used were equal to a vessel's fishing effort. For the estimates of the mean catch rate, this is equivalent to the sum of the total catch divided by the sum of the total effort within a stratum.

Various temporal and areal stratifications of the data have been considered. Monthly, quarterly, and annual stratifications are examined. When the data were stratified by area, geographic strata were defined as rectangular areas of 2.5° of latitude and 10° of longitude. These strata were chosen because preliminary analyses indicated that there was much greater variation both in effort and catch rates latitudinally than longitudinally. If smaller areas are selected, there tends to be too little data in many of the strata for meaningful analysis.

There are two statistical reasons for stratifying data: 1) to eliminate biases due to unequal distribution of sampling effort in strata with different means, and 2) to reduce the variance associated with the estimate of the mean. The first reason is a primary concern in calculating catch rates from fisheries data since the distribution of fishing effort both spatially and temporally is likely to be related to catch rates (i.e., fishermen probably concentrate on when and where the fishing is best).

In order to estimate an average catch rate for time periods and areas of interest, the estimates of the catch rates in the various strata need to be combined. For stratified data, an estimate of the average catch rate across strata is the weighted mean of the average catch rate within each stratum, where the weights are proportional to the magnitude of a stratum (Snedecor and Cochran 1967). The geographical and temporal stratifications presented below were considered to be equal in area and time. (This is not strictly true both because of land masses and differences in the length of a degree of longitude at different latitudes. For two of the geographical strata, the amount of land area of Papua New Guinea is large and these two strata should probably be given smaller weight in any extensions or refinements to the estimates presented below.) When all strata are of equal magnitude, the average catch rate across strata is the simple average of the within-strata estimates. Similarly, in this situation, an estimate of the variance is the average of the variance estimates for each stratum (Snedecor and Cochran 1967).

Because catch and effort statistics are not derived from a well-designed and controlled sampling experiment, there is not an a priori single best estimate for the average catch rate covering large areas and time periods. Thus, when considering estimates of the annual average catch rates, a set of different estimates based on various areal and temporal stratifications are presented. Comparison of the esti-

mates for different stratifications of the data may indicate possible sources of bias and can provide some indication of the robustness of any temporal trends suggested by any single set of estimates.

Another approach for dealing with possible biases due to unequal distribution of fishing effort is to calculate standardized catch rates using a general linear model (Gulland 1956b; Robson 1966; Allen and Punsly 1984). The advantage of this approach is that well-developed, standard statistical procedures can be employed to test for significant differences in catch rates over time where the effect of other factors on catch rates have been taken into account. Disadvantages of this approach include: 1) the data may be nonnormal even when transformed, 2) effects may not be simply additive (or multiplicative if a logarithmic transformation is used), and 3) the design matrix is almost always unbalanced and incomplete.

Extensive attempts were made to fit a general linear model to the catch rate data presented here. While the model was successful in greatly reducing the total sums of squares (e.g., an R^2 as high as 0.80), in all cases, the models included significant and large interaction effects between year and area, and between year and season. Such interactions are an indication of changes in availability and distribution between years and are not surprising given the large El Niño of 1983. When large interaction terms exist in a model, particularly when it is unbalanced and incomplete, direct interpretation of the main effects (in this case year) is problematical. An alternative to estimating the main effects in this situation is to develop μ_{ij}-models (Searle 1971) to compare directly the average effect between those combination of cells which are of interest. Conceptually this approach is similar to the stratified means approach developed above, but the calculation of the variance for the stratified means makes no assumption about the equality of the variance between cells. Because of the similarity of these two approaches and the problems with traditional general linear model estimates for unbalanced and incomplete data, the results of the general linear model have not been included in the present paper.

Interactions

The relationship between the longline and purse seine fisheries is considered in detail from two different approaches. In the first, catch rates of purse seiners and longliners operating in the same area during the same time period are compared. In this case a strong positive relationship would suggest that yellowfin tuna are a homogeneous stock with respect to the two fisheries. For this analysis, it is important that relatively fine scale temporal and area strata be used in order that differences in abundance between areas and time do not mask any relationship. Comparison of quarterly longline and purse seine catch rates are made for each individual 2.5° × 10° rectangular area in which there were at least five quarters with a reasonable amount of effort by both gears (i.e., 5 days of purse seine effort and 20,000 longline hooks).

The second approach involves the comparison of changes in longline catch rates in different areas to the purse seine catches that have occurred within these areas. This approach is a direct test of whether any reduction in longline catch rates can be detected as a result of the large catches by purse seiners. A fundamental assumption of this approach is that the stocks of yellowfin tuna within the areas being compared are largely spatially distinct or mixing only slowly. If the stock being fished is a homogeneous mixture, then no purse seine-induced differences between areas would occur.

For this second approach the percentage change in the average 1984–85 longline catch rate, relative to the average 1979–81 catch rate, are calculated for each of the 2.5° × 10° rectangular areas. The average catch rates within an area for the periods 1979–81 and 1984–85 were calculated as the simple average of the quarterly rates for an area. The percentage changes between these two periods are then examined in relation to past purse seine catches that have occurred in these areas. These two time periods were chosen for this comparison in order to see whether there has been differential and consistent long-term changes in abundances, and if so, whether these changes can be related to the distribution of purse seine catches.

It should be noted that these two approaches are meant to test for specific, possible localized interactions (either temporal or spatial). They are not meant as an exhaustive examination of the interactions between these two gears, but as feasible analyses given the short time series and limits of the current data.

RESULTS

Purse Seine Catch and Effort

Effort by Japanese purse seiners increased steadily through the first half of 1982 to around 450 days per month (Fig. 1A). Since 1982, levels of effort have remained relatively steady and have fluctuated

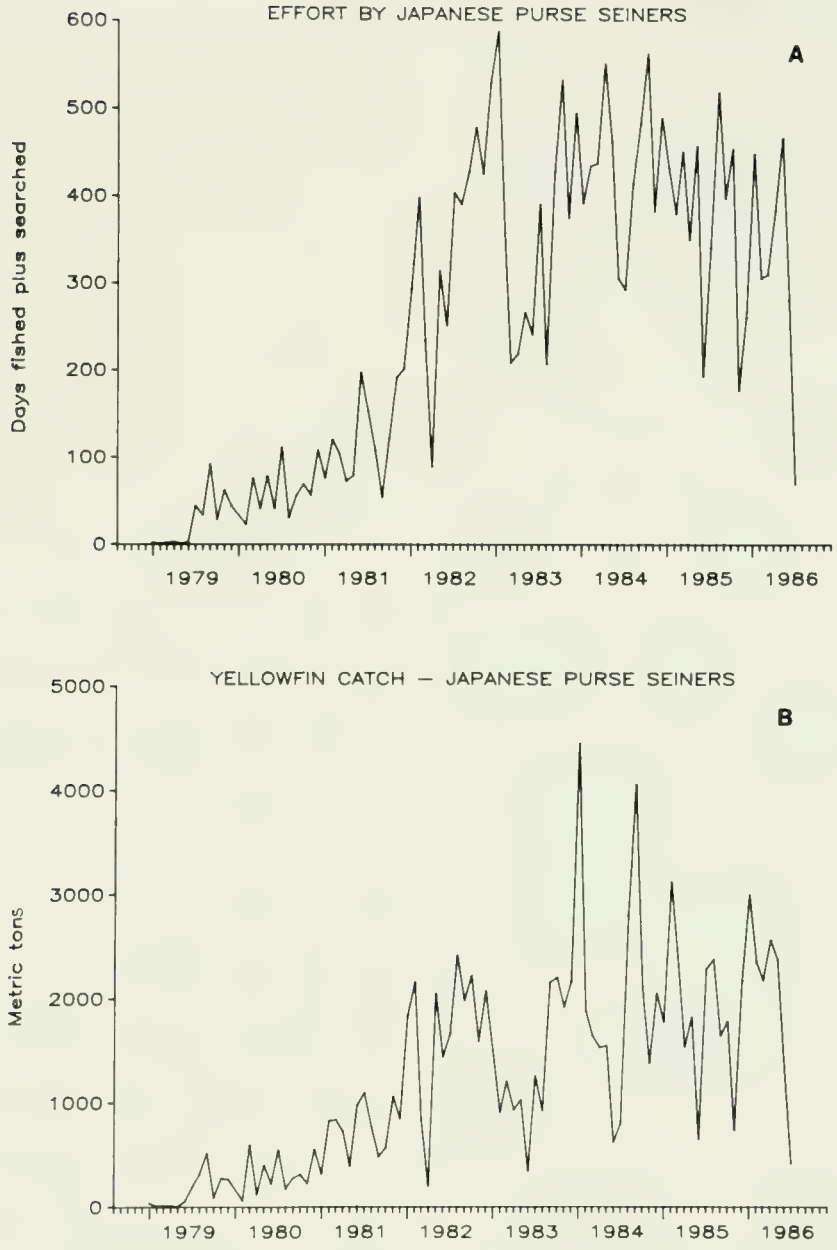


FIGURE 1.—Monthly catch of yellowfin tuna and effort statistics for Japanese purse seiners in the western Pacific based on data currently reported to the South Pacific Commission.

around this level. (Note that the apparent drop in effort for 1986 is an artifact due to time lags in receiving catch reports.)

The total catch of yellowfin by Japanese purse seiners roughly parallels the temporal distribution of effort (Fig. 1A, B). Overall, the corresponding catch rates have remained fairly constant with the lowest rates observed in 1983 (Fig. 2).

Table 1 presents a range of estimates of the annual catch rates for the various areal and temporal stratifications of the data. There are no consistent differences among the different stratifications

FIGURE 2.—Estimates of the monthly catch rates of yellowfin tuna for Japanese purse seiners (metric tons per day of effort) in the western Pacific. Error bars represent the estimates of one standard error.

TABLE 1.—Comparison of annual estimates of the overall average catch rate of yellowfin tuna (metric tons per day) by Japanese purse seiners in the western Pacific based on various areal and temporal stratifications of the data. Values in parentheses are estimates of standard error and *n* is the number of strata contained within each estimate. Stratum with less than five days of effort are not included.

Year	No areal or temporal stratification	Stratified by month	Stratified by quarter	Stratified by area	Stratified by quarter and area
1979	5.50	5.39	7.35	5.26	5.48
	(0.59)	(0.46)	(1.59)	(0.53)	(0.85)
	n = 1	*n* = 6	*n* = 4	*n* = 6	*n* = 9
1980	5.02	4.80	5.21	5.18	4.66
	(0.31)	(0.42)	(0.38)	(1.45)	(0.30)
	n = 1	*n* = 11	*n* = 4	*n* = 7	*n* = 13
1981	5.98	6.35	6.18	4.15	5.34
	(0.32)	(0.38)	(0.32)	(0.39)	(0.51)
	n = 1	*n* = 12	*n* = 4	*n* = 15	*n* = 29
1982	4.82	4.74	4.97	4.69	4.91
	(0.23)	(0.22)	(0.23)	(0.60)	(0.34)
	n = 1	*n* = 12	*n* = 4	*n* = 11	*n* = 24
1983	3.83	3.89	3.74	3.24	3.48
	(0.20)	(0.21)	(0.20)	(0.29)	(0.27)
	n = 1	*n* = 12	*n* = 4	*n* = 14	*n* = 25
1984	4.77	4.75	4.85	3.70	3.39
	(0.23)	(0.16)	(0.20)	(0.20)	(0.17)
	n = 1	*n* = 12	*n* = 4	*n* = 13	*n* = 36
1985	5.04	5.09	5.00	4.61	5.36
	(0.25)	(0.20)	(0.22)	(0.24)	(0.26)
	n = 1	*n* = 12	*n* = 4	*n* = 18	*n* = 41
1986	6.26	6.26	6.19	4.84	5.26
	(0.32)	(0.30)	(0.32)	(0.29)	(0.27)
	n = 1	*n* = 7	*n* = 3	*n* = 15	*n* = 21

within a year. The larger differences that do exist tend to include stratification by area. If a normal distribution is assumed, the only significant differences at a 0.05 probability level among the stratifications within a year (i.e., 1981, 1984, and 1986) would be in stratifications which include area.

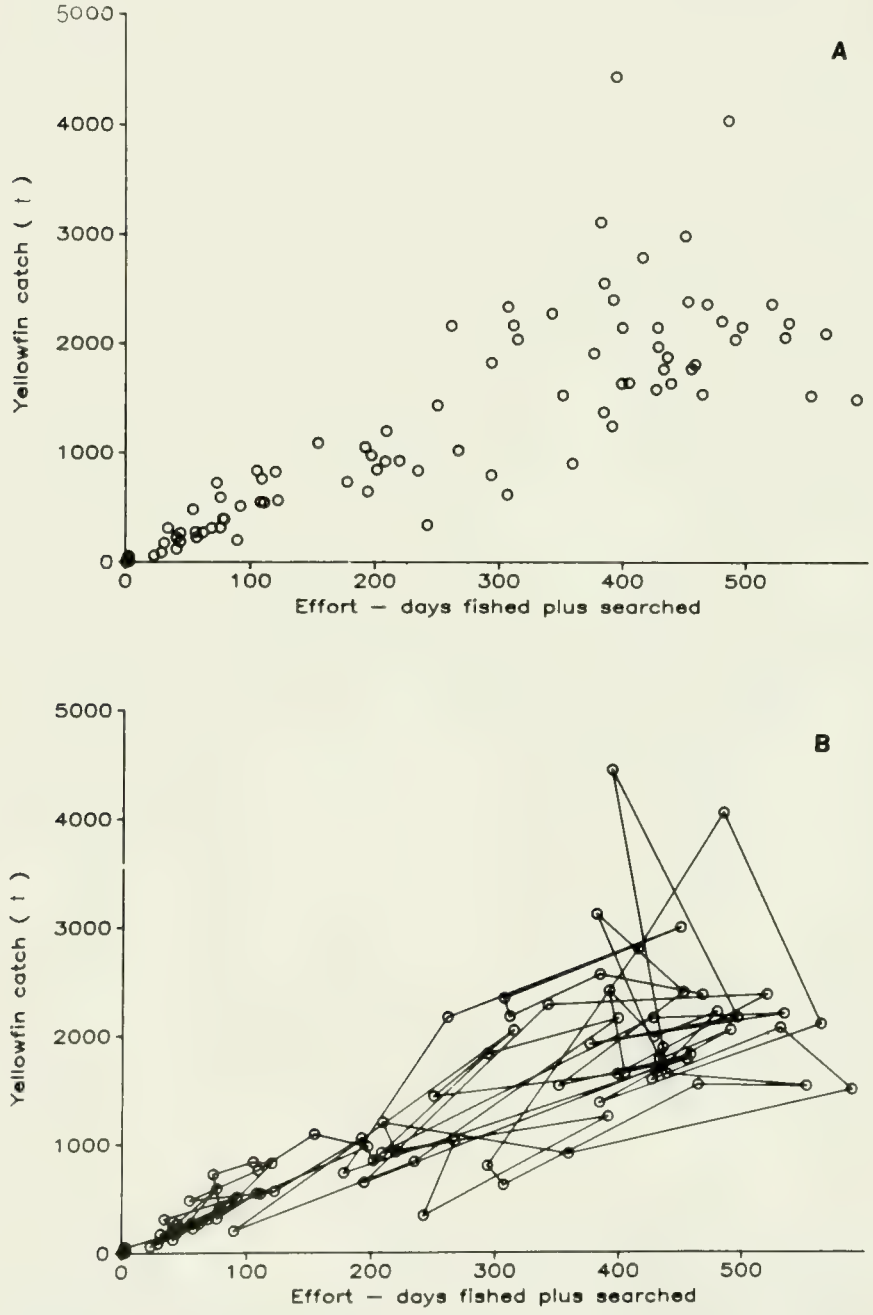


FIGURE 3.—The relationship between monthly yellowfin tuna catch and effort by Japanese purse seiners. The points have been connected in the temporal sequence in which they occur.

However, for estimates stratified by both area and season, only the 1984 estimate would be significantly different from any of the other stratified means within a given year. A lack of consistent differences among the various stratifications within years does not mean that siginificant area and seasonal differences may not exist, but only that whatever effects may exist tend to balance in the present data.

Among the various annual estimates in Table 1, the estimates for 1983 tend to be the lowest (perhaps reflecting the large El Niño of that year), while those for 1979 and 1986 tend to be the highest. While the length of the time series is short, there is no indication within any of the stratifications of an overall temporal trend in the annual estimates.

Relationship Between Purse Seine Catch and Effort

A production plot of total monthly catch versus total monthly effort suggests that monthly catch rates can be highly variable and that months with the highest effort tend to have lower catch rates (Fig. 3). Thus, the catch rates in the 6 months in which the total effort exceeded 500 days of effort are all below the overall mean catch rate (Fig. 4) and the average of the catch rate for these 6 months is 38% below the mean catch rate for all 77 months. However, the results in Figure 3 should not be interpreted in terms of a general catch curve because the changes in catch rates associated with change in effort appear to be too large to be a reflection of the overall population dynamics (see Discussion). These lower catch rates at higher effort levels are not as apparent when a quarterly stratification of the data is considered (Fig. 5), and there is no evidence for these lower rates with an annual stratification (Fig. 6). Caution is warranted in interpreting any of these figures as general catch curves since they are not based on total catch and effort statistics for the yellowfin tuna surface fisheries (most significantly, the lack of information from the United States and other eastern Pacific vessels). Also, note that for all of the catch curves, statistics from 1986 are not included because of current incompleteness of currently available data.

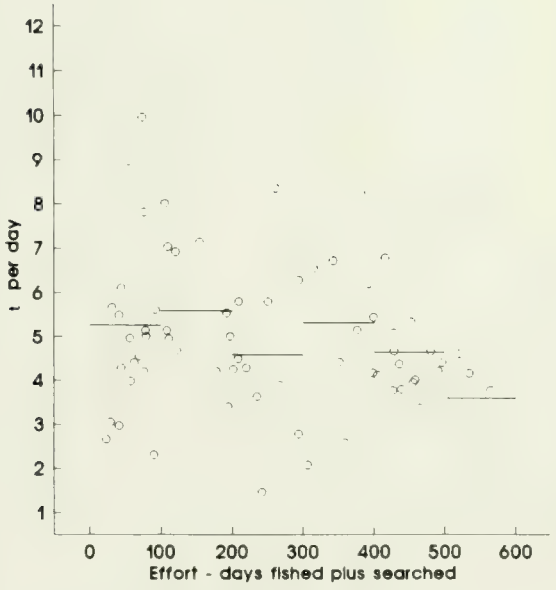


FIGURE 4.—The relationship between monthly catch rates (metric tons per day) and fishing effort of yellowfin tuna by Japanese purse seiners. The horizontal lines represent the mean catch rate for each 100 day range of effort.

Longline Catch and Effort

Effort by Japanese longliners has been relatively constant, but with some decline in recent years. However, a large amount of monthly variation occurred, with a suggestion of seasonal periods of reduced effort during the second half of the year (Fig. 7A). Catches also exhibit a large amount of monthly variation, but suggest a declining trend since 1982 (Fig. 7B). As with the purse seine statistics, the drop in catch and effort in 1986 is due to the time lag in receiving catch reports. There has been a general decline in the average hooking rate since 1979–80, except for 1983 (Fig. 8).

Comparison of estimates of the average annual catch rates of yellowfin tuna for various combinations of temporal and area stratification shows a consistent temporal pattern (Table 2) which is similar to the pattern shown by the monthly rates in Figure 8. The annual estimates of the average catch rate tend to be highest in 1983, and the lowest estimates occur either in 1985 or 1986. The high catch rates in 1983 might be related to a change in vulnerability as a result of the large El Niño which occurred during this year. The 1985–86 estimates are about 33% below the 1979–80 levels. Whether overall the catch rates in this short time series indicate a general decline depends critically upon the interpretation given to 1983 catch rates (see Discussion).

Similar to the purse seine estimates, there is no consistent pattern among the stratified annual

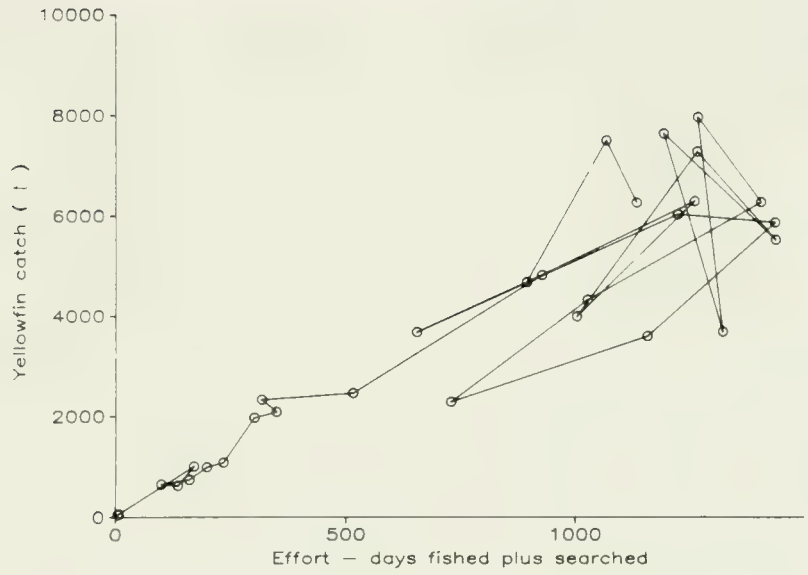


FIGURE 5.—The relationship between Japanese yellowfin tuna catch and purse seine effort based on quarterly statistics. The points have been connected in their temporal sequence.

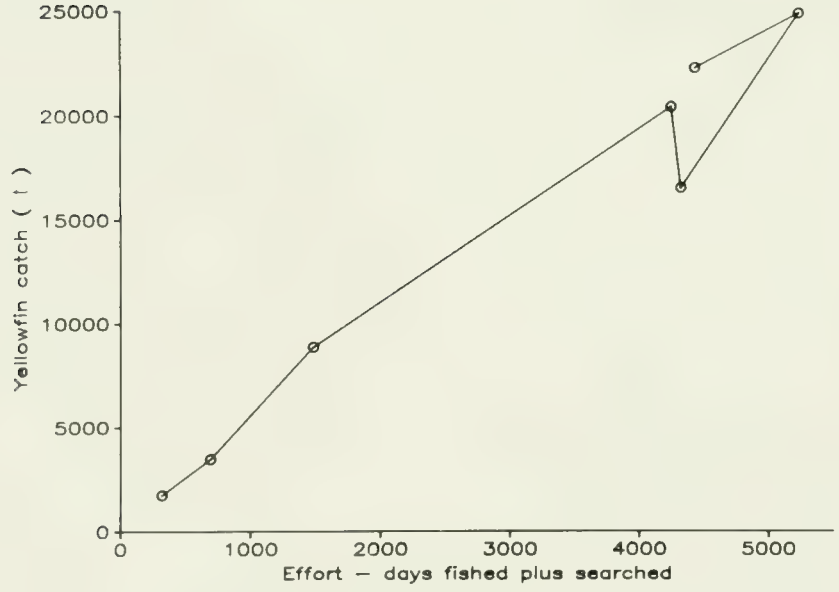


FIGURE 6.—The relationship between Japanese yellowfin tuna catch and purse seine effort based on annual statistics. The points have been connected in their temporal sequence.

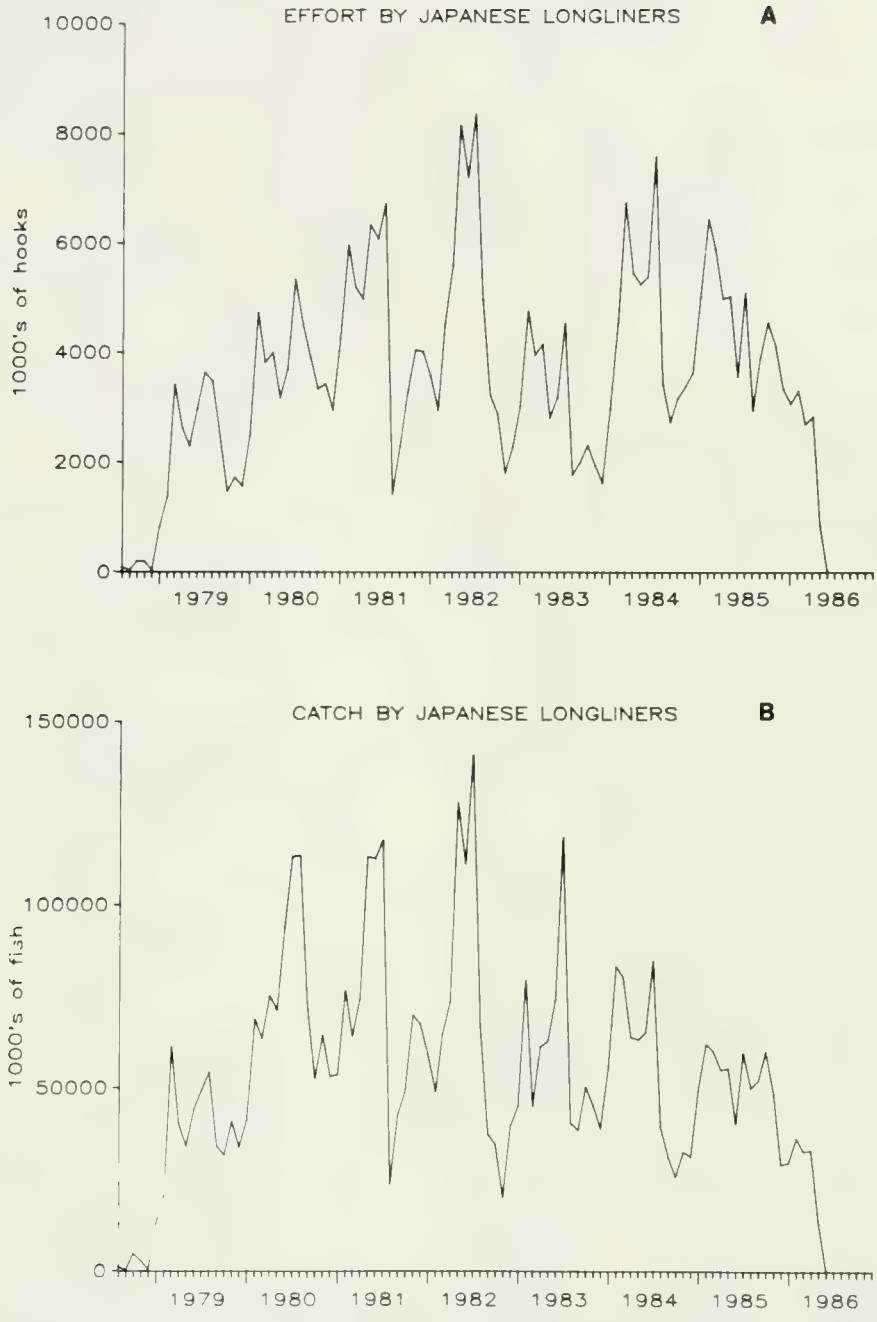


FIGURE 7.—Monthly catch of yellowfin tuna and effort statistics for Japanese longliners in the western Pacific based on data currently reported to the South Pacific Commission.

FIGURE 8.—Estimates of the monthly catch rates for Japanese longliners (number of yellowfin tuna per 1,000 hooks) in the western Pacific. Error bars represent estimates of one standard error.

TABLE 2.—Comparison of annual estimates of the overall average catch rate of yellowfin tuna (number/1,000 hooks) by Japanese longliners in the western Pacific based on various areal and temporal stratifications of the data. Values in parentheses are estimates of standard error and *n* is the number of strata contained within each estimate. Stratum in which less than 20,000 hooks a set were not included.

Year	No areal or temporal stratification	Stratified by month	Stratified by quarter	Stratified by area	Stratified by quarter and area
1978	16.47	13.53	14.06	17.30	17.65
	(2.10)	(1.36)	(1.79)	(1.45)	(1.32)
	$n = 1$	$n = 5$	$n = 2$	$n = 10$	$n = 11$
1979	16.43	16.90	17.17	18.16	16.66
	(0.27)	(0.27)	(0.27)	(0.41)	(0.25)
	$n = 1$	$n = 12$	$n = 4$	$n = 38$	$n = 106$
1980	19.42	19.25	19.23	18.35	18.40
	(0.29)	(0.23)	(0.27)	(0.43)	(0.29)
	$n = 1$	$n = 12$	$n = 4$	$n = 45$	$n = 145$
1981	15.79	15.88	15.95	13.96	13.60
	(0.22)	(0.18)	(0.20)	(0.18)	(0.17)
	$n = 1$	$n = 12$	$n = 4$	$n = 42$	$n = 146$
1982	14.81	14.48	14.67	12.50	12.60
	(0.23)	(0.19)	(0.22)	(0.15)	(0.15)
	$n = 1$	$n = 12$	$n = 4$	$n = 41$	$n = 143$
1983	19.38	19.99	20.10	17.42	18.54
	(0.35)	(0.29)	(0.32)	(0.28)	(0.36)
	$n = 1$	$n = 12$	$n = 4$	$n = 43$	$n = 120$
1984	12.09	12.06	11.84	12.58	12.40
	(0.23)	(0.18)	(0.20)	(0.28)	(0.17)
	$n = 1$	$n = 12$	$n = 4$	$n = 44$	$n = 149$
1985	11.35	11.54	11.51	11.08	11.12
	(0.19)	(0.16)	(0.18)	(0.17)	(0.15)
	$n = 1$	$n = 12$	$n = 4$	$n = 41$	$n = 146$
1986	11.41	11.99	11.73	10.71	10.88
	(0.33)	(0.34)	(0.34)	(0.30)	(0.27)
	$n = 1$	$n = 5$	$n = 2$	$n = 37$	$n = 58$

estimates within years. If a normal distribution is assumed, most of the differences among the different stratifications within a year would not be significant at the 0.05 probability level. As with the purse seine data, the lack of differences in the annual estimates should not be interpreted to mean that area and temporal effects do not exist.

Fine-Scale Relationship Between Purse Seine and Longline Catch Rates

Comparison of catch rates by longliners and purse seiners in the same area and during the same time period suggests that there is little relationship between them (Fig. 9). Thus, for all the rectangular areas in which there were at least five quarters with a reasonable amount of effort by both gear types, the correlation coefficient between the catch rates for the two gear types ranges from −0.37 to 0.89 (Table 3). When the variances associated with the individual catch rates are taken into account (e.g., Figure 9), there is nothing to suggest that these correlation coefficients are not zero.

TABLE 3.—Estimates of the correlation coefficients for the quarterly yellowfin tuna catch rates between Japanese longliners and purse seiners within rectangular areas of 2.5° of latitude by 10° of longitude.

Coordinate southwest corner of the area	Correlation coefficient	Number of quarters
7.5°N, 140°E	0.62	10
7.5°N, 130°E	0.89	5
5.0°N, 140°E	0.53	20
5.0°N, 130°E	0.12	13
2.5°N, 150°E	0.00	9
2.5°N, 140°E	−0.07	24
2.5°N, 130°E	−0.11	8
0.0°N, 150°E	−0.09	12
0.0°N, 140°E	0.10	25
2.5°S, 150°E	−0.37	14
2.5°S, 140°E	−0.25	22
5.0°S, 140°E	0.34	11

Changes in Longline Catch Within Areas Relative to Purse Seine Catches

A comparison of the percentage change in the 1984–85 yellowfin tuna hooking rate from the 1979–81 rate within an area suggests that the observed changes are not related to the magnitude of the purse seine catches (Fig. 10). In Figure 10, the percentage changes are compared with the purse seine yellowfin tuna catch from 1979 to 1983 in order to allow for a time lag due to the differential size or capture in the two gears. Similar results are obtained if different time frames are used for the purse seine catches. The spatial distribution of these percentage changes suggests that the largest decline in longline catch rates has occurred in the western and northern borders of the area fished by longliners (Fig. 11). This area overlaps, but tends to be outside of the areas of major Japanese purse seine catches (Fig. 12).

DISCUSSION

Effect of Different Stratifications

For both the longline and purse seine fisheries for yellowfin tuna, the different stratifications yielded relatively consistent patterns for the annual changes in catch rates. For the purse seine rates, the fact that different temporal stratifications had little effect on the overall annual averages is not surprising given the relatively equal temporal distribution of effort within a year (i.e., any seasonal differences in catch rates will be given approximately even weight in the pooled estimates).

Stratifications by area could have been expected to have a large effect on the annual purse seine catch rates given the highly clustered distribution of effort during any given month (Fig. 13; unpubl. results). The ratio of an unstratified catch rate estimate to a stratified estimate has been defined as a concentration index by Gulland (1955). A value near 1 for this ratio is usually interpreted to mean that fishermen are not concentrating their fishing effort in area and time strata where fish are most abundant. Values for this index based on the values in Table 1 range from 0.82 to 1.39. While there is some tendency for the annual estimates of catch rates which include stratification by area to be less than the unstratified estimates, the lack of any large and significant differences is due to the fact that there is almost no effort outside of these areas of high concentration. Thus, the data even when stratified, adds little information on catch rates outside the specific areas being fished at any given time.

For the longline results, the value of Gulland's concentration index ranges from 0.9 to 1.18 when calculated from the values in Table 2. In this case the lack of any large differences between the stratified and unstratified estimates in Table 2 is not due to effort being concentrated in only a few strata, but may be related to the multispecies aspect of the

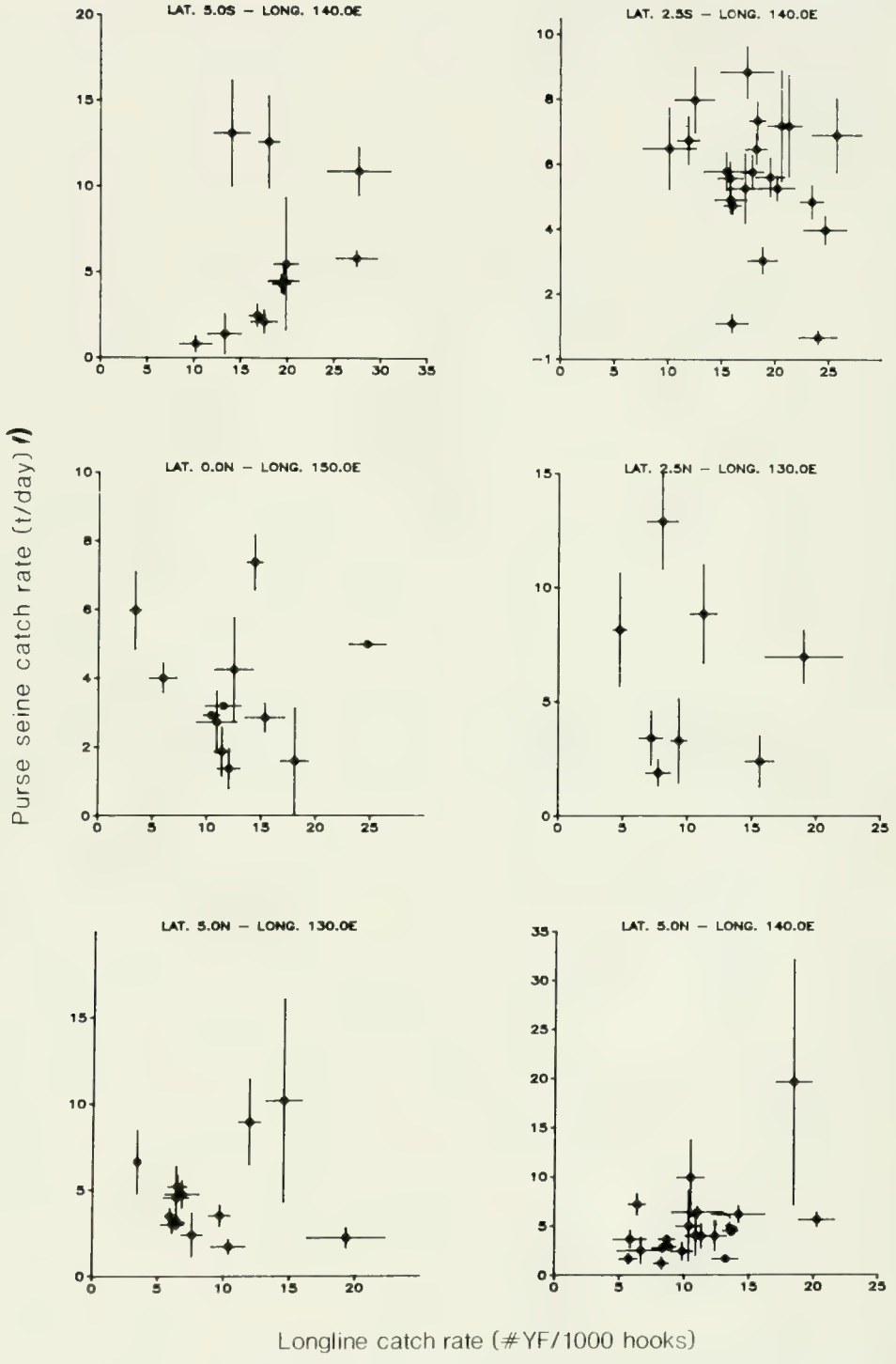


FIGURE 9.—The relationship between quarterly yellowfin tuna catch rates by Japanese longliners and purse seiners within rectangular

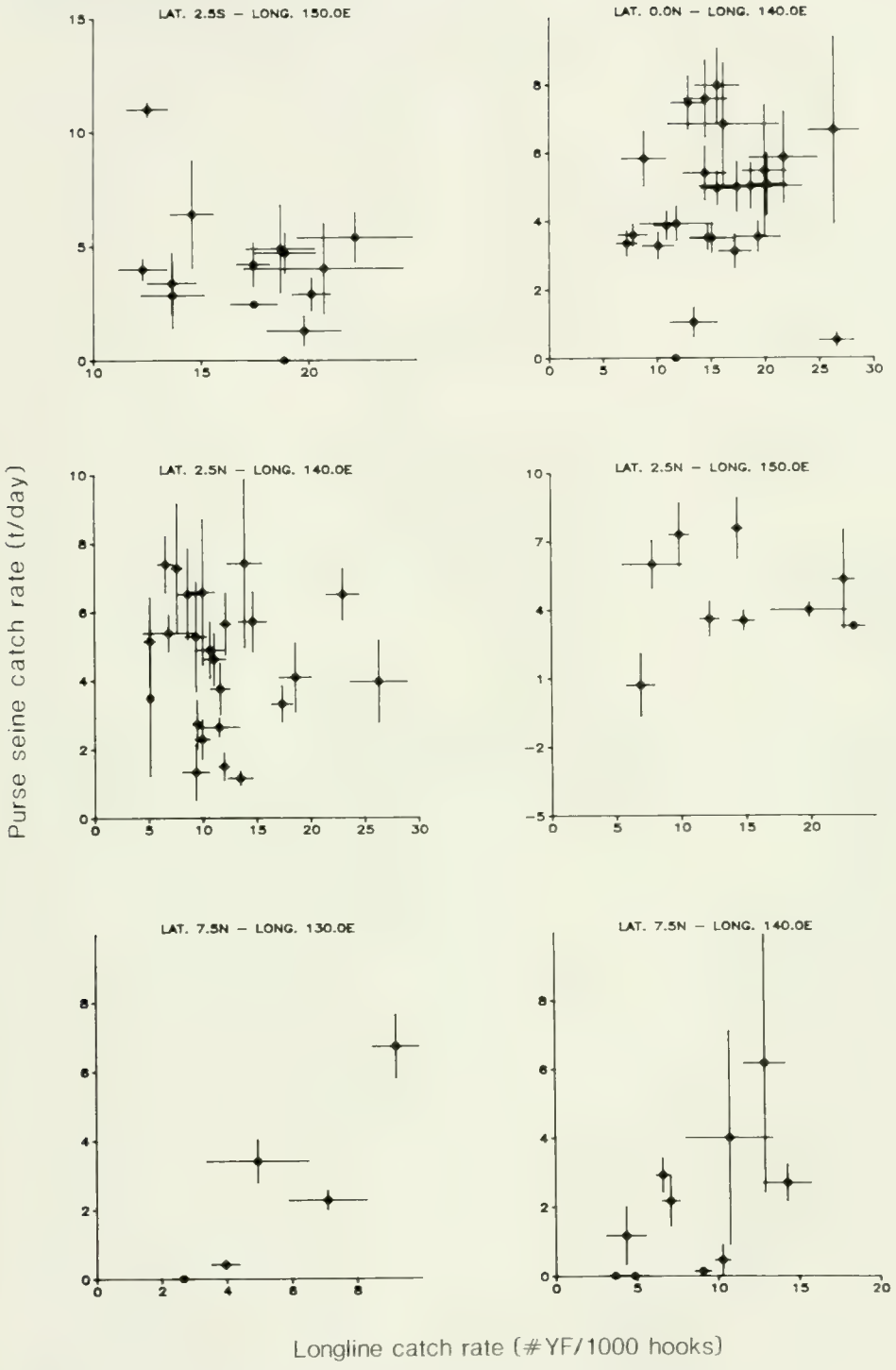


FIGURE 9.—*Continued*—areas of 2.5° of latitude and 10° of longitude. Error bars represent estimates of one standard error.

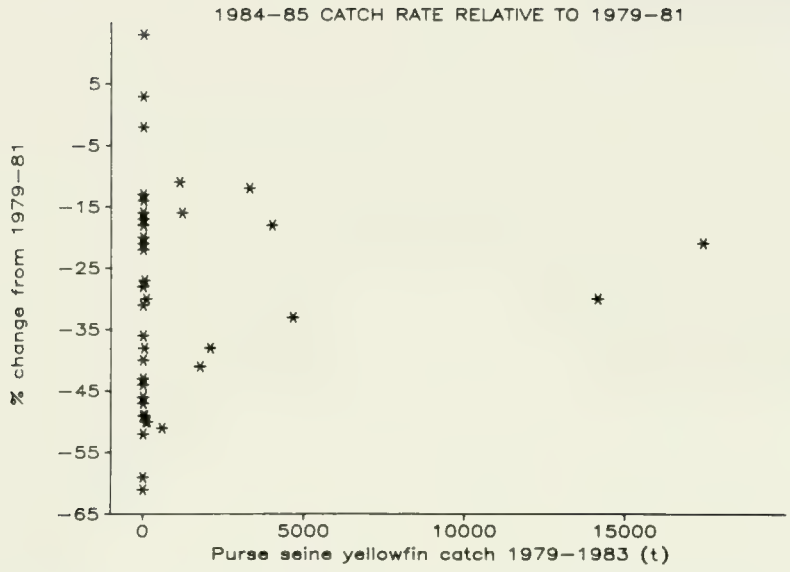


FIGURE 10.—The relationship between yellowfin tuna catches by Japanese purse seiners and the percentage change in yellowfin longline catch rates for rectangular areas of 2.5° of latitude by 10° of longitude in the western Pacific.

longline fishery. Thus, concentration indices for the combined catch of the major tuna species are generally greater than the value for any individual species (unpubl. results).

Purse Seine

The results of this paper suggest that there is no evidence that the western Pacific yellowfin tuna surface stocks vulnerable to purse seining have declined. Catch rates have remained relatively constant despite a 10-fold increase in catches since 1978. However, some cautions are warranted in interpreting the catch rates from this fishery in terms of indices of abundances. There are a number of factors specific to this fishery which are likely to result in nonlinear relation or lack of relation between changes in catch rates and changes in the size of the population. These could result in catch rates remaining high despite significant changes in abundances. Many of these have been discussed previously in connection with catch rates for schooling populations and for purse seine gear (e.g., Neyman 1949; Paloheimo and Dickie 1964; Quinn 1980; Mangel 1982; Gulland 1983). Probably the most important factor for the Japanese purse seine fishery is that a high proportion of the catch comes from early morning sets on naturally occurring flotsam (called logs by the fishermen) or manmade, free-floating fish aggregating devices (referred to as payao's in recognition of their Philippine origin). Generally, Japanese purse seiners tend to make a single early morning set on a log or payao located the previous day. Often vessels will return to the same log or payao over a period of several weeks (Gillett 1986; Farman 1987). Thus, purse seine catch rates will be a function both of the density and detection rate for logs and more importantly the renewal rate of fishable tuna schools under a log. Little is known about any of these processes, but they are not likely to be a simple linear function of yellowfin tuna densities.

Other factors which also might cause a nonlinear relation between catch rates and population density are the nonrandom distribution of searching effort and the sharing of fishing information among vessels. The fact that the concentration indices of Gulland discussed above are generally low does not indicate that the nonrandom distribution of searching effort (e.g., Figure 12) is not a major concern. Purse seine effort during any given month occurs only in a small portion of the range for surface yellowfin tuna. Thus, even when stratified by area, it is not possible to determine whether the catch rates are representative of overall abundance.

The catch curves based on monthly and quarterly statistics (Figs. 3, 5) might be interpreted as contradicting the above conclusions that there is no

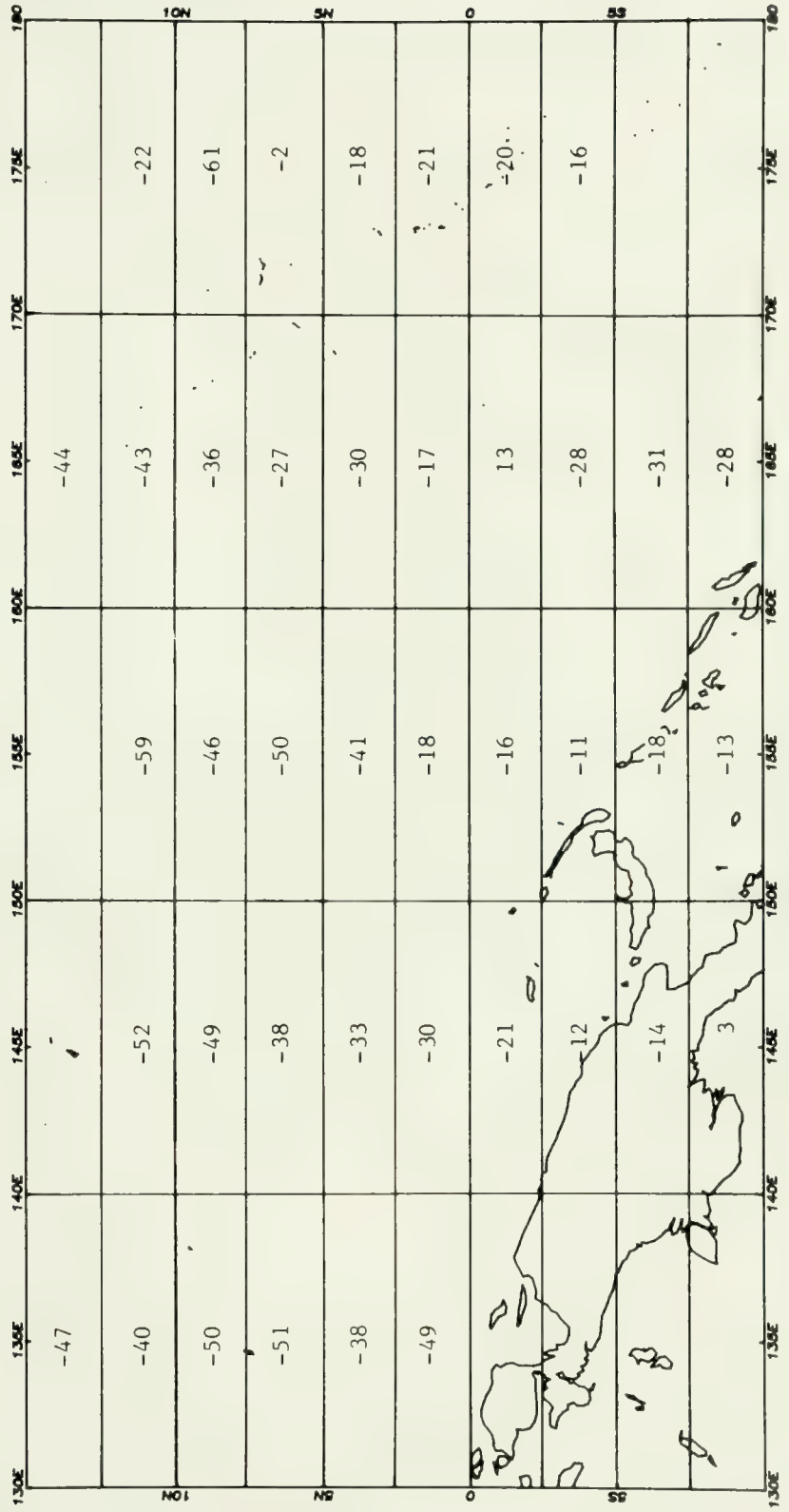


FIGURE 11.—The percentage change in the yellowfin tuna catch rate by Japanese longliners for 1984–85 relative to 1979–81 by rectangular areas.

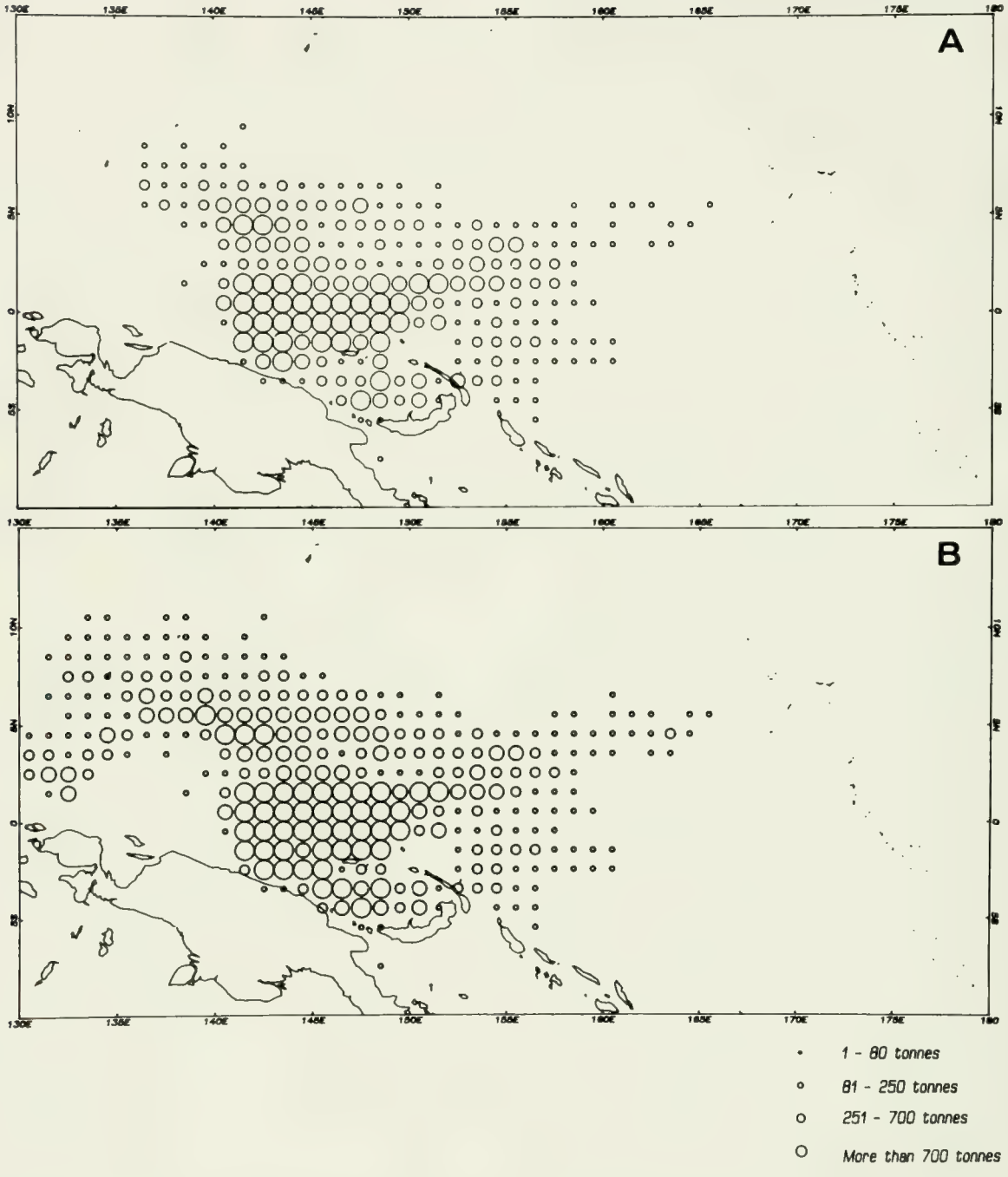


FIGURE 12.—The distribution of Japanese yellowfin tuna purse seine catches by one degree square: A) 1979 to 1983; B) 1979 to 1985.

evidence that surface yellowfin tuna stocks have declined. However, the time sequence of changes in catches in relation to changes in effort are not those that would be expected if these catch curves were a reflection of the overall population dynamics. Thus, when the temporal sequence of changes in catch and effort are considered by connecting the points in Figure 3, the resulting pattern suggests that during a time interval of one month, a large change in effort results in correspondingly large changes in the catch rates. If these changes in catch rates reflected changes in the overall yellowfin tuna abundance, it would mean that catches of 3,000–5,000 t represented a very significant proportion of the total yellowfin tuna stock and that a very rapid recovery of the yellowfin tuna stocks (i.e., during the course of a month) can occur with reductions in effort. Neither of these conclusions seem reasonable. Also, the fact that there is no evidence that catch rates are lower at the highest effort levels so far experienced when the data are combined into annual statistics, further suggests that the catch curves based on monthly and quarterly statistics do not reflect the overall population dynamics.

The apparent reduction in catch rates at the highest effort levels based on the monthly or quarterly stratification is an interesting phenomenon warranting further investigation. The reduction in catch rates at these highest effort levels does not appear to be the result of increased handling time at higher effort levels. The number of sets per day has remained relatively constant and unrelated to the total number of days fished. Two possible explanations for the decline in monthly catch rates with higher effort are localized depletions and interactions with skipjack tuna catches. In this regard, it is interesting to note that monthly or quarterly catch curves for skipjack tuna, *Katsuwonus pelamis*, from this same fishery do not show this apparent decline in catch rates at highest effort. The lack of decline in the catch rate for skipjack tuna is another indication that the decline observed for yellowfin tuna is not due to handling time.

Longline

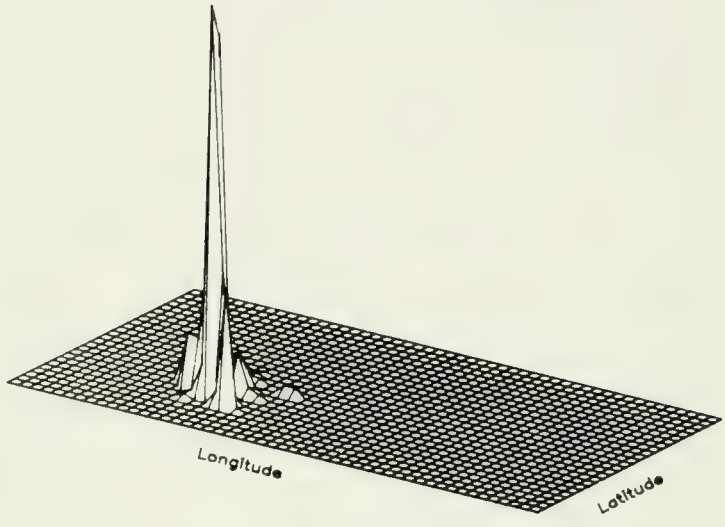
Longline catch rates in 1984 and 1985 are substantially lower than those in 1979. Whether this decrease represents a general long-term decline is not possible to determine without a longer time series of data. Interpretation of the temporal trend depends partially upon whether the observed rates in 1983 are attributable to the large El Niño of 1983 or whether they are a measure of the random variability in the fishing process. The magnitude of the increase observed in 1983 is much larger than might be expected given the observed variability both between and within months (the latter is indicated by the error bars in Figure 8). While it is tempting and even reasonable to attribute the high rates in 1983 as an El Niño effect, the length of the current time series and available information on the effects of El Niño on yellowfin tuna are insufficient to objectively resolve whether the high 1983 rates are the results of El Niño.

Caution in interpreting longline catch rates as directly reflecting changes in population abundances is also warranted. While the operational procedures in tuna longlining would appear not to be very susceptible to inducing a nonlinear relationship between abundance and catch rates (i.e., handling time is not a major factor and the length of a single longline insures that effort can not be highly concentrated in space). However, concerns have been raised about potential hook competition at higher densities (Rothschild 1967; Au 1985). More importantly, longliners target different depths depending upon local conditions, market factors and the relative abundance of different species. In addition, the fact that surface catches in the Atlantic were able to greatly exceed previous catches of large yellowfin tuna by longliners despite the fact that longline catch rates had declined steeply suggests that the relationship between availability to the different gears versus overall abundance is not simple (Fonteneau 1981).

In order to gain a broader temporal perspective to compare the current catch rates, longline hooking rates from 1962 to 1980 for the same area considered in this paper are plotted in Figure 14 based on published data by the Fisheries Agency of Japan (1962–80). Longline hooking rates were generally declining through the mid-1970s and then appear to have entered a period of recovery. Because of the commencement of the purse seine fishery in 1980, interpretation of the overall long-term temporal trend is confounded and depends upon whether the apparent increase in the 1970s was a true recovery or a reflection of the variability that can be expected in this fishery.

Interaction

The results presented in this paper suggest that the relation between longline and purse seine fisheries is complex. The above discussion indicates that the current data is insufficient to determine whether a general decline is occurring in longline catch rates.



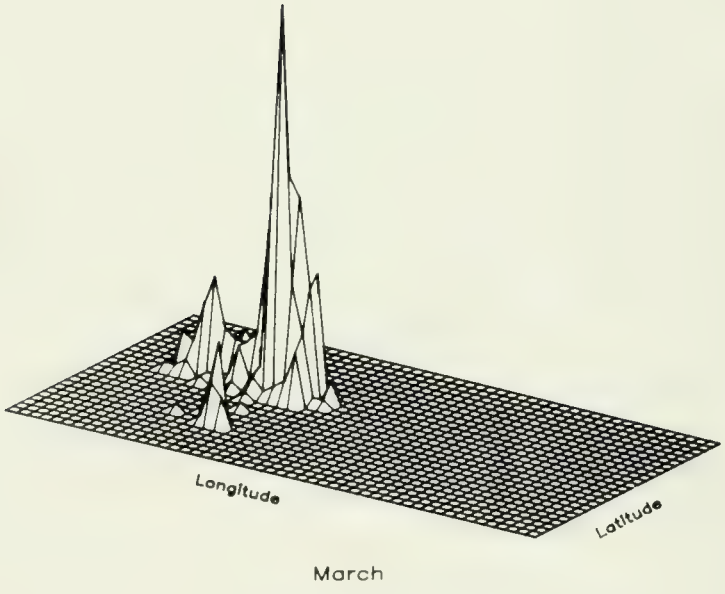
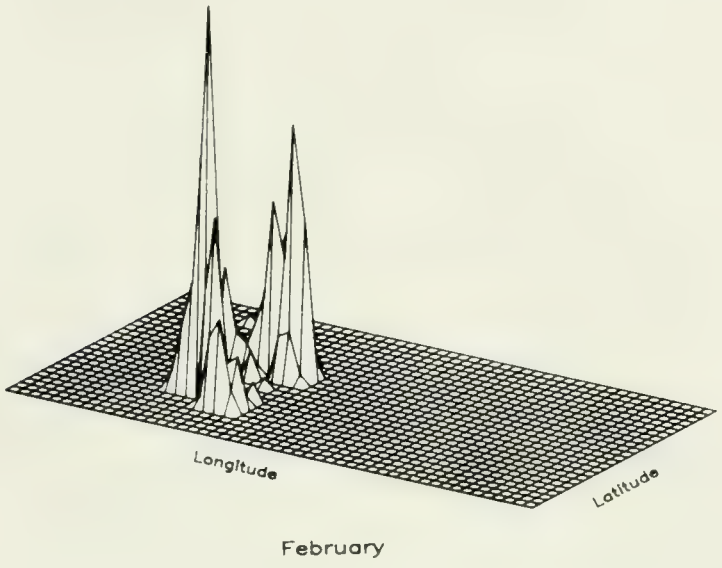


FIGURE 13.—Examples of monthly prospective block drawings showing the distribution of fishing effort by one degree square for Japanese purse seiners. The



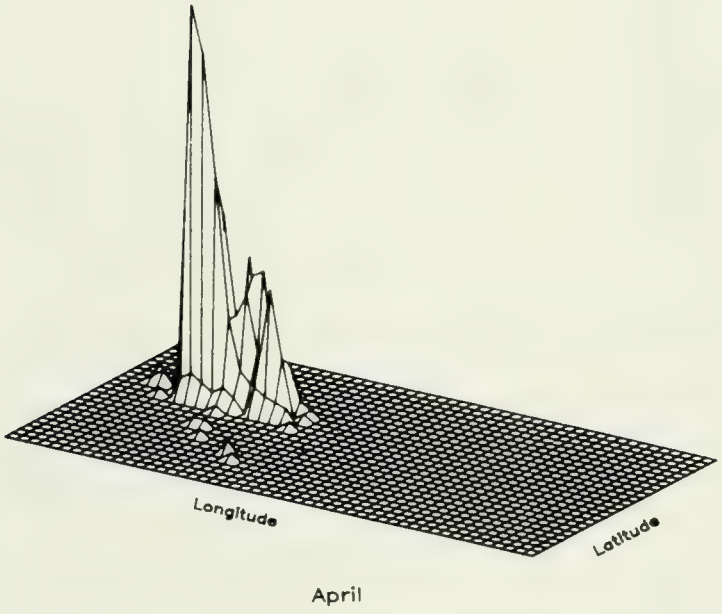


FIGURE 13.—*Continued.*—figures presented are for the first four months of 1984. The boundaries of the area are from lat. 10°S to 15°N and long. 130°E to 180°E.

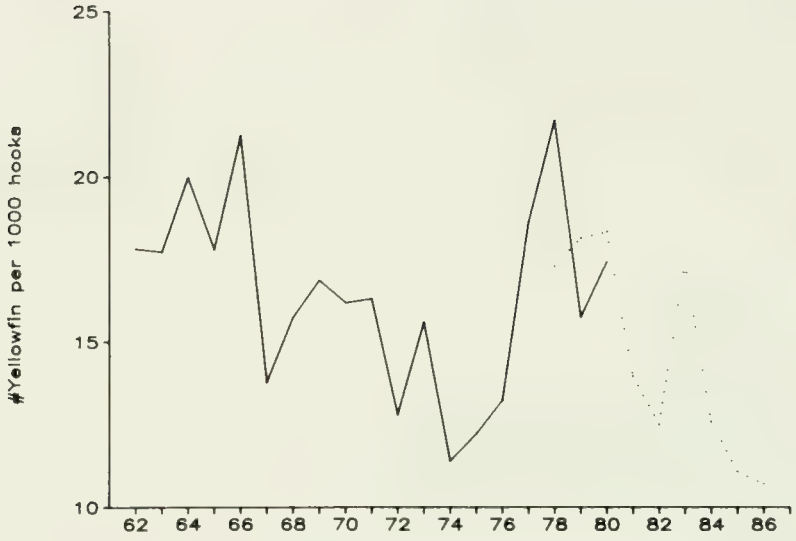


FIGURE 14.—Estimates of annual catch rates for Japanese longliners (number of yellowfin tuna per 1,000 hooks) in the western Pacific. The solid line represents stratified estimates based on five degree square areas from published data by the Fisheries Agency of Japan (1962–80). The dotted line represents the estimates stratified by area from Table 5 based on data held by the Tuna and Billfish Assessment Programme of the South Pacific Commission.

Even if a general decline is occurring, it would not be possible to evaluate whether the purse seine catch is a likely cause of the decline without either more detailed information on the age structure of the catches or a much longer time series of data.

Based on the comparison of catch rates within the same area and time period, yellowfin tuna do not appear to be a homogeneous stock with respect to purse seining and longlining. The lack of any relationship at a fine spatial and temporal scale could be due to

1. factors affecting vulnerability to surface gear are unrelated to factors affecting vulnerability to longline gear, or
2. those portions of the yellowfin tuna population being exploited by the purse seine fishery (i.e., primarily 2–3 year old fish) have a spatial-temporal distribution which does not coincide with that for the older and larger yellowfin tuna being harvested by longliners.

In reality, probability both of these factors, plus random elements in the fishing process are contributing to the apparent lack of any relationship.

The fact that the observed changes in longline catch rates within areas appear not to be related to the purse seine catches taken from that area may be due to any number of factors. Some possible hypotheses include

1. The level of exploitation by purse seiners within any of the areas considered has been insufficient to affect a significant decline in longline catch rates.
2. Given the difference in the size and age of the fish exploited by the two fisheries, a time lag would be expected before any effect could be observed and the presently available time series may be too short to detect the effects.
3. There is a large amount of movement of yellowfin tuna so that the yellowfin being harvested by longliners are not merely the escapement from the purse seine fishery within that area.
4. There are two independent stocks or substocks of yellowfin tuna—a deep and a surface one—each of which is primarily vulnerable to only one gear type.
5. The available purse seine catch statistics are incomplete and areas in which the greatest decline in longline catch rates have occurred may in fact be areas where large, unreported purse seine catches have occurred.
6. The main areas in which the largest decline in longline catch rates have occurred border the EEZ's of the Philippines and Indonesia. The

Philippine surface tuna fishery has increased dramatically and there is a suggestion that overfishing has occurred there (Floyd and Pauly 1984).

It is not possible with existing knowledge to distinguish between these hypotheses while available data suggest that all of the above may be contributing to the observed results. Thus, for example, very limited tagging data from the western Pacific suggest that the yellowfin tuna stocks may be very large and that yellowfin tuna caught by longliners in the Pacific can travel long distances from their initial place of capture. Ten yellowfin tuna tagged by the SPC were recaptured by longliner and traveled an average distance of 1,280 miles from their point of release (unpubl. data). Tag experiments from the Atlantic yielded no returns by longliners which suggests that yellowfin tuna cannot be considered as a single homogeneous stock in that ocean with respect to the different gears (Fonteneau 1981). Yet, the fact that surface tagged fish have been recaptured by longliners in the Pacific means that they are not totally distinct. A better understanding of the interactions between longline and purse seine fisheries is dependent upon both a more complete set of catch and effort statistics and a longer time series of data, plus biological information from other sources. The present low longline catch rate and the importance of longline fisheries in the South Pacific make this a question of immediate concern.

ACKNOWLEDGMENTS

The catch and effort data base used in the analyses in this paper would not exist without the cooperation and help of the fisheries officers from the individual island states of the western Pacific. Their efforts are gratefully acknowledged. In addition, present and past staff of the Tuna and Billfish Assessment Programme of the South Pacific Commission were instrumental in the creation and maintenance of this data base and also provided useful reviews and comments on drafts of this manuscript. I also wish to thank Veronica van Kouwen for her help in the preparation of this manuscript.

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SEASONAL SPAWNING CYCLE, SPAWNING FREQUENCY, AND BATCH FECUNDITY OF THE CABEZON, *SCORPAENICHTHYS MARMORATUS*, IN PUGET SOUND, WASHINGTON[1]

ROBERT R. LAUTH[2]

ABSTRACT

The seasonal spawning cycle, spawning frequency, and batch fecundity of the cabezon, *Scorpaenichthys marmoratus*, were studied in Puget Sound, Washington, USA between September 1984 and October 1985 using scuba techniques. Seasonal embryo mass abundance and ovarian condition indicated that the spawning season started in November and continued 10 months through the following September while peak spawning activity occurred during March and April. Three factors revealed in this study indicated that females may spawn more than once during a single spawning season: 1) the presence of an intermediate mode of yolked oocytes, 2) a low wet gonadosomatic weight index, and 3) a protracted spawning season. Batch fecundities predicted from regressions on weight and length ranged between 66,000 and 152,000 eggs for females from 2.5 kg to 10.5 kg and between 57,000 and 137,000 eggs for females from 500 mm to 775 mm.

Out of approximately 300 cottid species worldwide (Nelson 1984), the cabezon, *Scorpaenichthys marmoratus*, is perhaps the largest (Jordan and Everman 1898) and can attain a length of 990 mm and a weight of 11.4 kg (Feder et al. 1974). Cabezon range from Pt. Abrejos, Baja California (Miller and Lea 1972) to Samsing Cove near Sitka, AK (Quast 1968). Their depth range in California is from nearshore tidepools to 76 m (Feder et al. 1974). Cabezon are demersal and solitary and are usually associated with reefs, boulders, or beds of kelp, algae, or eelgrass.

A small recreational fishery exists for cabezon. For divers who spearfish, cabezon are prime targets because of their trophy size, desirable food qualities, and general vulnerability in shallow nearshore habitats. Knowledgeable anglers also enjoy catching and eating cabezon even though they are not generally targeted (Olander 1984).

Although cabezon are not targeted by a commercial fishery at present, they are incidental in commercial catches and they do occasionally appear in fish markets along the west coast (Ayres 1854; O'Connell 1953; personal observations in fish markets in Seattle, WA).

There is little published information on cabezon reproductive biology aside from a life history study in Monterey, CA done by O'Connell (1953), studies of cabezon roe toxicity (Fuhrman et al. 1969, 1970; Hashimoto et al. 1976; Hubbs and Wick 1951; Pillsbury 1957), and diving observations of cabezon nesting behavior in a California kelp forest (Feder et al. 1974). Spawning season, spawning frequency, and batch fecundity of cabezon north of California have to date, not been studied. Thus, it seems prudent that we learn about the reproductive biology of cabezon in other areas, especially because of their value as a fishery resource. The objective of this study was to examine the spawning ecology of cabezon in Puget Sound, WA and to make a geographical comparison with data for cabezon in California.

METHODS AND MATERIALS

Study Sites

Sampling consisted of transect and collection dives. Sampling began in September 1984 and ended in October 1985 and was done using scuba techniques. Edmonds Underwater Park and the Edmonds Marina breakwater, both located in Edmonds, WA, USA (lat. 47°48′N, long. 122°22′W; Fig. 1), were chosen as study sites because they had been previously identified by the author as spawning areas for cabezon. Two transects, each covering 250 m^2, were established along a scuttled dry dock at Edmonds Underwater Park. Transect 1 was the remains of the northern bulkhead of the drydock

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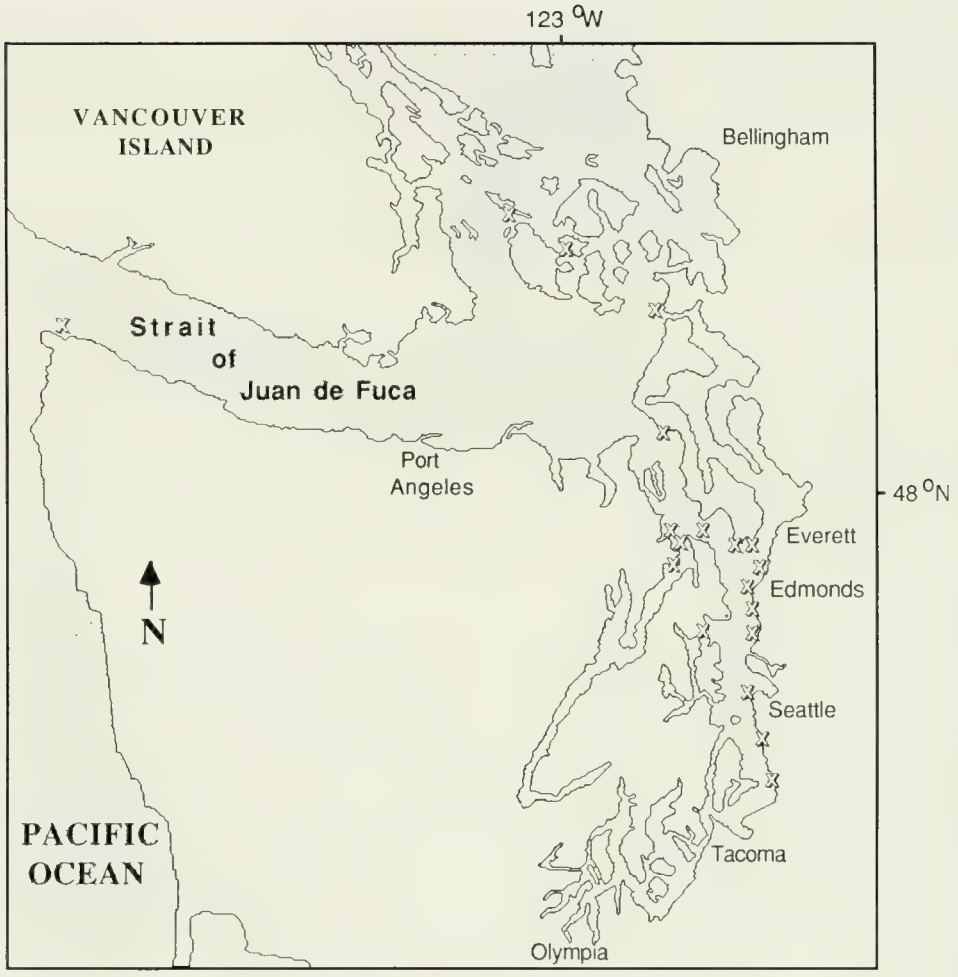

FIGURE 1.—Map of Puget Sound, Washington, USA showing the general location of scuba sampling sites (X).

and was 65.5 m long and 3.8 m wide. The southern half of the drydock, designated Transect 2, was 30 m south of Transect 1 and was 55 m long by 4.5 m wide. The eastern and western ends of both Transects 1 and 2 were in 6.0 m and 9.0 m of water (MLLW, i.e., Mean Lower Low Water), respectively.

Transect 3 was a portion of the Edmonds Marina breakwater parallel to a Washington Department of Fisheries' fishing pier. The transect was 150 m in length by 5 m in width and covered a total area of 750 m^2. The breakwater consisted of large basalt boulders that extended from 3 to 5 m (MLLW) below the surface of the water. In addition to the breakwater, the transect included a sandy area with interspersed boulders to a depth of 7 m (MLLW).

Transect and Collection Dive Sites and Procedures

Each transect was sampled at least once a month. Dives were made more frequently when spawning activity increased. Fifty transect dives totalling 46 hours of bottom time were made. Physical data collected on each dive included water temperature and depth. Biological data gathered included number of cabezon and number and depth of embryo masses. Dives in spawning areas were made during all hours of daylight. Collection of specimens for biological data was by pneumatic speargun. Forty-eight collection dives totalling 36 hours of bottom time were made. Fifty female cabezon were collected throughout Puget Sound, including areas in the Strait of

Juan de Fuca and San Juan Islands (Fig. 1). All specimens captured were weighed to the nearest 0.1 kg and total length measured to the nearest mm.

Processing of Ovaries

From 1 to 10 females were sampled each month so that the progression of ovarian development could be followed throughout the study period and spawning frequency could be determined. Entire ovaries were excised, weighed to the nearest 0.1 g, put in gauze bags, and placed in modified Gilson's solution to harden the eggs and to break down ovarian tissue (Simpson 1951).

After 5 to 6 months in Gilson's solution, the eggs from each ovary were separated from the ovarian tissue using a mild jet of water while passing them through a series of Tyler[3] brass sieves with openings of 1.651 mm, 0.295 mm, 0.180 mm, and 0.075 mm. Most eggs with diameters less than 0.075 mm passed through the smallest screen and were discarded. Loose eggs were retained by the sieves and stored in jars with 5% formalin.

Ova Diameter Frequencies

Eggs and water (2.5 L) were homogeneously mixed in a 4 L beaker with magnetic stirrer. A random 5 mL subsample was drawn with a pipette and the eggs were measured with a calibrated ocular micrometer.

At least 200 eggs were measured from each ovary. Ova diameters were grouped using 0.05 mm increments as midpoints. Based on ova diameter frequency histograms, ovaries were grouped into eight stages (I-VIII). Ranges, means, medians, and standard deviations were calculated for the apparent modes within each stage.

I calculated a wet gonadosomatic weight index (WGSI) for each female using the formula of Gunderson and Dygert (1988). The WGSI's for each stage of ovarian development were averaged and used as a measure of relative gonadal investment of females.

The Number of Eggs to be Spawned

The subsampling procedure for estimating the number of eggs to be spawned was identical to the one for measuring ova diameters. Subsamples were enumerated using a dissecting microscope, a gridded petri dish, and a laboratory counter. When modes in an ovary overlapped, the number of eggs from the largest mode were counted twice and averaged. At least three subsamples were taken for each ovary and the mean total number of eggs to be spawned was calculated, using a simple volumetric proportion. If the coefficient of variation was greater than 10%, additional subsamples were made until it dropped below 10%.

Unweighted least-squares linear regression was used to predict the total number of eggs to be spawned using lengths and weights of females as independent variables. All regression analyses were done with a personal computer according to methods described by Kleinbaum and Kupper (1978).

RESULTS

Seasonal Embryo Mass Abundance

The beginning and end of the spawning season were defined as the dates when embryo masses were first and last seen. During 19 collection and transect dives throughout Puget Sound from mid-September until the end of November, no cabezon embryo masses were observed. The first embryo mass observed in Puget Sound was on 6 December 1984. A sample of eggs from this embryo mass was placed in a 5 gal bucket filled with seawater and most hatched within 30 minutes. The eggs were apparently near the end of their incubation period since little of the yolk sac was remaining. Based on work from this study, incubation time until hatching is several weeks, thus the embryo mass was most likely deposited sometime in middle or late November 1984.

Along Transects 1, 2, and 3, embryo masses were first observed on 2 January 1985 and 7 and 21 December 1984, respectively. After the first embryo masses appeared, there was a steady increase in abundance with some fluctuation (Fig. 2). The peak number of embryo masses at all three transects occurred during March and April 1985, after which there was a general decline. By 30 August 1985, embryo masses were totally absent from Transects 1 and 2 and by mid-September 1985, none were found at Transect 3 or elsewhere in Puget Sound.

Between November 1984 and September 1985, there were 35 embryo masses observed on Transect 2, 23 embryo masses on Transect 1, and 15 embryo masses on Transect 3. It is possible that some embryo masses may have hatched or disappeared (e.g., predation, cannibalism, dislodged by physical dis-

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

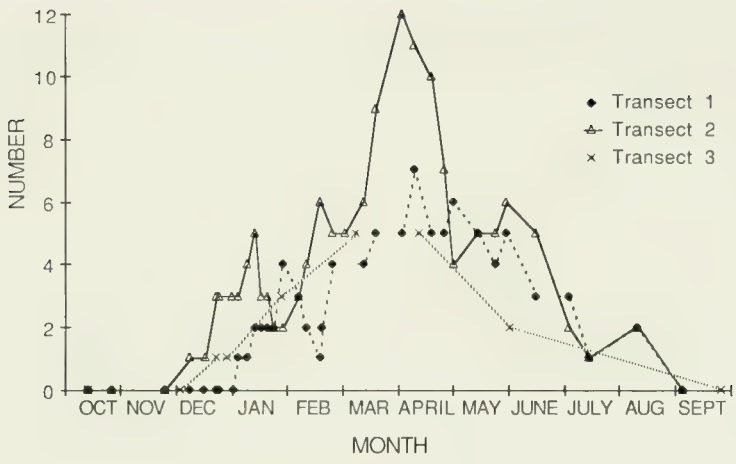

FIGURE 2.—Temporal fluctuation in the abundance of cabezon embryo masses at Transects 1, 2, and 3.

turbance) between dives; thus the totals may have been underestimated.

It was assumed that incubation time of eggs till hatching was the time between when an embryo mass was first observed and when hatching was first noted. For 13 nests that were monitored from 21 January to 26 May 1985, incubation time ranged between 25 and 49 days and averaged 34 days with a standard deviation of 6.8 days. Water temperature varied between 8° and 10°C during this period.

Embryo masses were found in the intertidal to depths of 17 m and were deposited on hard substrates including wood pilings and logs, rocks, and steel. Embryo masses were always observed on exposed surfaces rather than underneath structures or inside crevices.

Spawning Frequency

Ova diameter frequency plots were used, in part, to determine the frequency of spawning. Eight stages of ovarian development, designated I to VIII, were delineated based on the modal configurations of ova diameter frequency plots (Fig. 3). Seven ovaries were in Stage I, characterized by relatively small resting oogonia with diameters ≤0.40 mm (Fig. 3I). The bulk of the eggs from Stage I were translucent, devoid of yolk, and had diameters ≤0.20 mm. Eggs of this size and with these characteristics were present in all eight stages.

Stage II ovaries were found in six cabezon (Fig. 3II). In addition to the large reserve of resting oogonia, there was another mode of opaque eggs which averaged 0.46 mm and ranged from 0.35 to 0.65 mm.

Stages III to VII represented two basic types of female spawners: those which were going to spawn for the first time (Stages III to V) and those which had already spawned once and had the potential for spawning again (Stages VI and VII). For both groups (spawned and unspawned), there were two groups of yolked oocytes.

There were seven female cabezon with Stage III ovaries (Fig. 3III). Besides the resting oogonia, there was an intermediate mode (average 0.47 mm, range 0.35 to 0.65 mm) which represented a reserve group of immature oocytes for future spawning, and a larger mode (average 0.84 mm, range 0.70 to 1.10 mm) which consisted of maturing ova destined to be spawned within the current spawning season. In Stage IV, egg hydration was beginning and the largest mode was more distinct than in Stage III ovaries (Fig. 3IV). The largest mode of yolked oocytes averaged 1.23 mm and ova diameters ranged from 1.00 to 1.45 mm in Stage IV ovaries.

For females with Stage V ovaries, spawning was imminent and there was no evidence of prior spawning (Fig. 3V). The modal configuration of an ova diameter frequency plot of a female captured while actually spawning was Stage V. For all Stage V ovaries combined, the average diameter of the largest mode (hydrated eggs) was 1.48 mm and the range was from 1.35 to 1.65 mm. Eggs from the intermediate mode had an average diameter of 0.55 mm and ranged from 0.35 to 1.0 mm.

Stage VI ovaries were characteristic of recently

spawned females (Fig. 3VI). Three females with Stage VI ovaries were collected in the immediate vicinity of freshly deposited embryo masses, presumably after spawning them. Within these ovaries, an incipient mode, which ranged in size from 0.70 to 0.95 mm and had a mean size of 0.79 mm, was apparent. A relatively small number of large diameter eggs (~1.5 mm) were scattered within all Stage VI, Stage VII, and Stage VIII ovaries (Fig. 3VI–VIII) and were presumably remnants of the recent spawning event. In Stage V females the largest mode would mask evidence of residual eggs so it was not possible to ascertain whether they had already spawned in the 1984–85 spawning season.

As the ovaries progressed to Stage VII, the eggs of the incipient mode were larger and distinct from the intermediate mode. These yolked eggs appeared to be hydrating in preparation for another spawning. Females exhibiting this condition had spawned previously and since eggs of an intermediate size were still present, these females were capable of spawning again. The incipient mode for Stage VII ovaries ranged from 0.95 to 1.50 mm with a mean of 1.16 mm. The intermediate mode of Stage VII ovaries ranged from 0.35 to 0.90 mm and averaged 0.51 mm.

Stage VIII ovaries were similar to Stage I ovaries. There was a single and small mode of eggs which were deteriorating noticeably. Irregularly shaped ova were translucent or transparent and devoid of yolk. Unlike Stage I, Stage VIII ovaries had remnant eggs (~1.5 mm in diameter) from at least one previous spawning event (Fig. 3VIII).

When the eight stages were plotted against the date when females were captured, a general progression of ovarian development was seen (Fig. 4). Stage III to V ovaries were only seen in females caught between December and May. Stages VI and VII were found from February through August. Stage VIII females were caught both before and after Stage III through VII females. The early Stage VIII's were probably carry-overs from the previous spawning season. Females in Stages I and II were found prior to all other stages.

The WGSI values for the eight stages of ovarian development were in agreement with what might be expected in a multiple spawner (Fig. 5). For ovaries in the resting condition (Stage I), the WGSI was at its lowest point. The WGSI gradually increased to a maximum in Stage V when eggs were hydrated and females were in spawning condition. After the eggs were released there was an obvious drop in the weight of the ovaries relative to the body weight. The WGSI slightly increased in Stage VII and then fell in Stage VIII. Without the aid of histological techniques, it was not possible to distinguish an intermediate stage between VII and VIII; this stage would have been virtually identical to Stage V, and had there been such a stage, it is conceivable the WGSI would have reached another maximum before finally declining in Stage VIII.

Relation Between Batch Fecundity and Weight and Total Length

From ova diameter frequency plots, two basic types of female spawners were evident: 1) those which were going to spawn for the first time (unspawned; Stages III to V), and 2) those which had already spawned at least once and had potential for spawning another batch (spawned; Stages VI and VII). The number of eggs to be spawned during each spawning event (batch fecundity) was determined by estimating the number of eggs in the largest mode for females possessing ovaries in stages III to VII.

Data for spawned and unspawned females was pooled for regression analysis because the range of values for comparable fish weights and lengths was similar, and because separate regressions for spawned and unspawned females were not statistically different ($P > 0.05$). Furthermore, pooling spawned and unspawned data provided analysis over a broader size range of fish and considerably increased the sample size. The resulting regressions of batch fecundity on length and weight were significant at $P < 0.001$, and the correlation coefficients were 0.69 and 0.73, respectively (Fig. 6). The regression of batch fecundity on length predicted that females from 500 mm to 775 mm would release between 57,000 and 137,000 eggs during a spawning event, and the regression of batch fecundity on weight predicted that females from 2.5 kg to 10.5 kg would release between 66,000 and 152,000 eggs during each spawning event.

DISCUSSION

Along the western U.S. coast, the length of the spawning season for marine cottids varies from 1 month to year-round (Atkinson 1939; Jones 1962; Marliave 1975; Tasto 1975; DeMartini 1978; DeMartini and Patten 1979; Goldberg 1980; Garrison and Miller 1982). Based on temporal embryo mass abundance and ovarian condition, cabezon spawning in Puget Sound commences in late November and lasts 10 months through early September of the following year while peak spawning occurs from

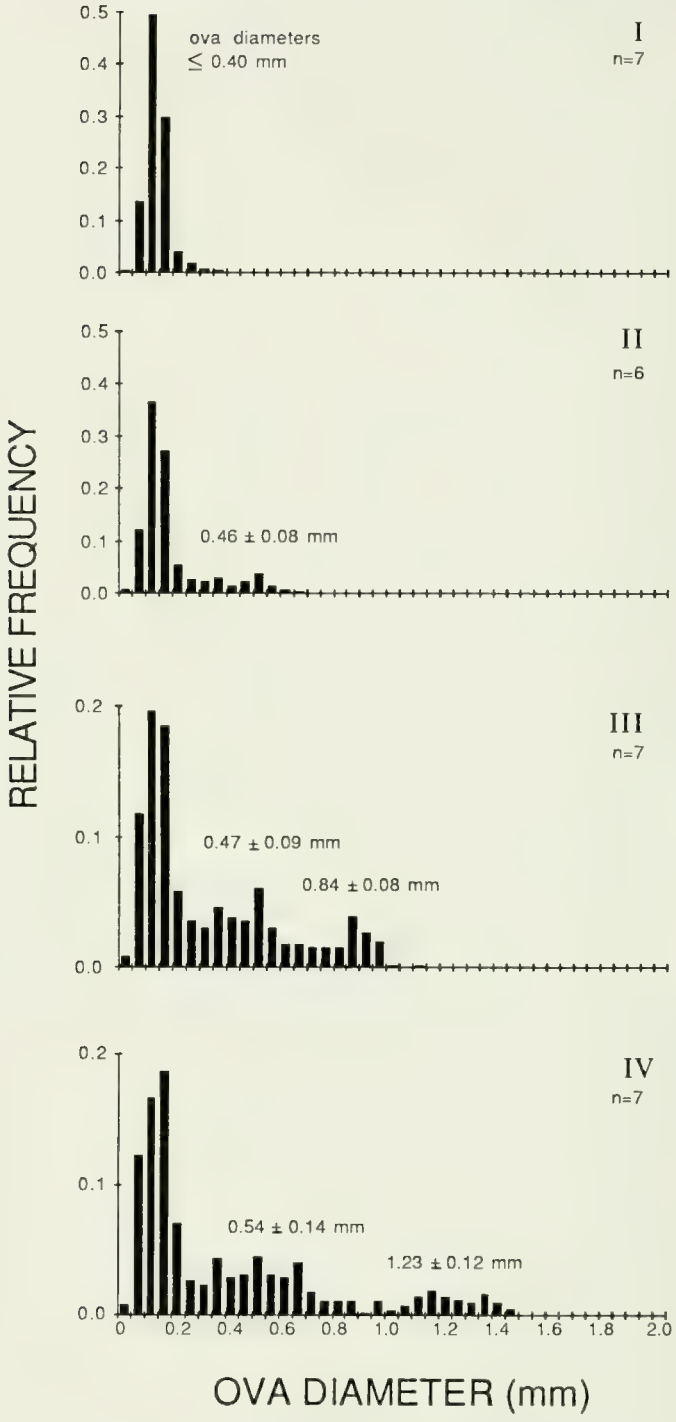

FIGURE 3.—Eight stages of ovarian development (Stages I to VIII) based on the modal configuration of ova diameter frequency plots.

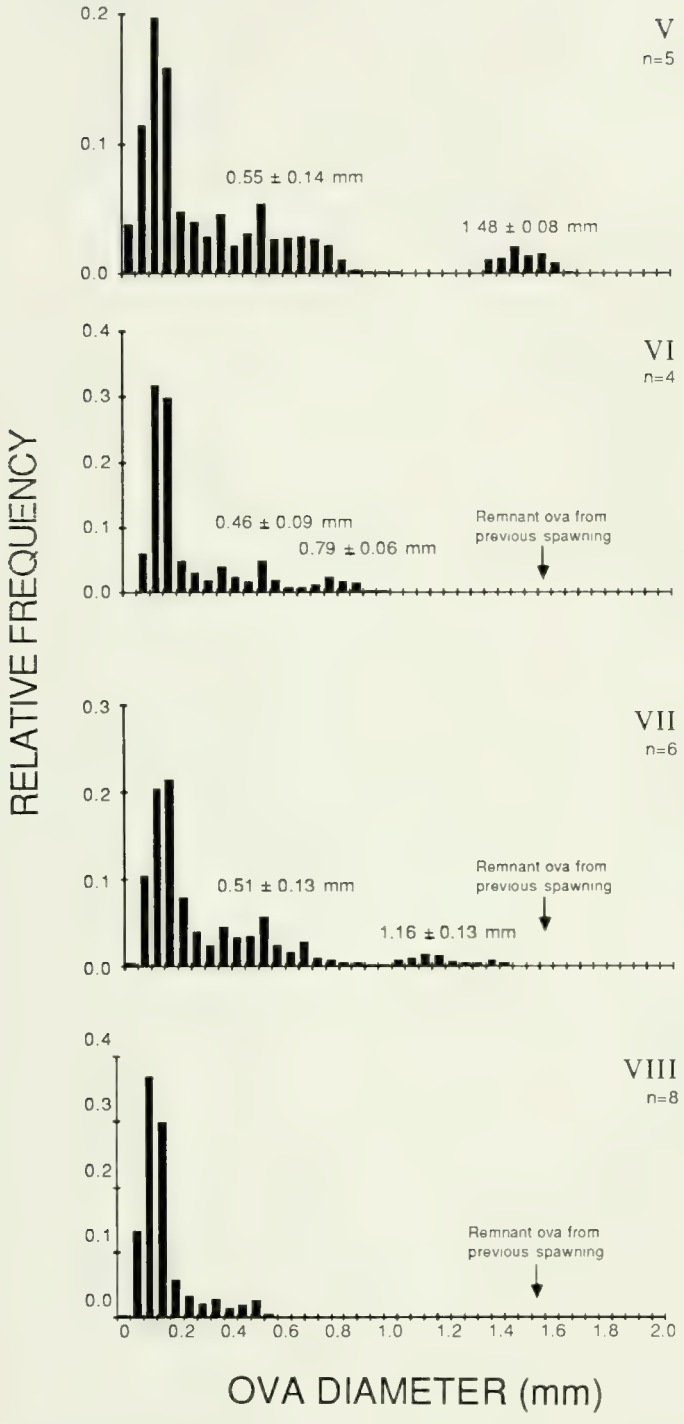

FIGURE 3.—*Continued.*—Modal average ±1 standard deviation are listed above each mode.

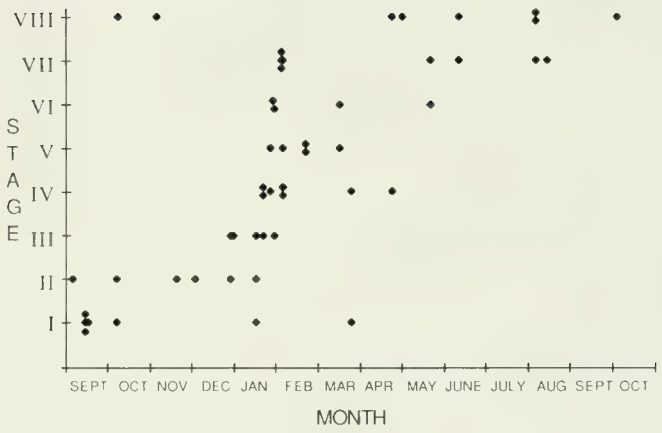

FIGURE 4.—Stage of ovarian development versus time of capture.

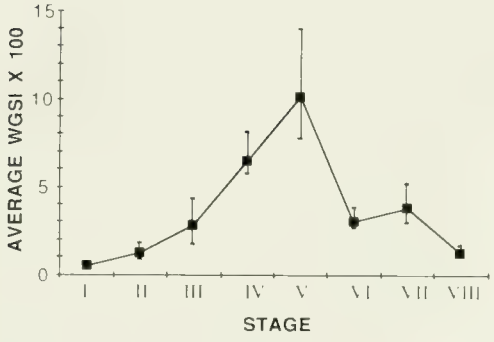

FIGURE 5.—Average wet gonad-somatic weight index (WGSI) × 100 versus stage of ovarian development. Vertical bars represent the 95% confidence limits.

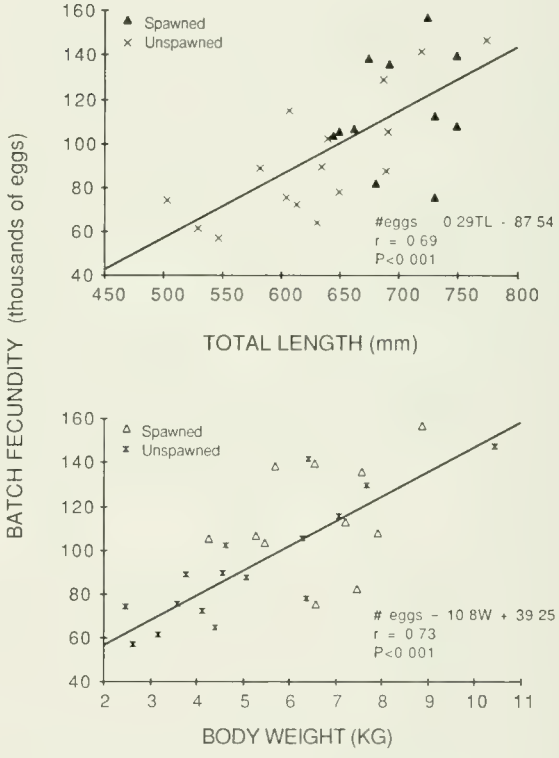

FIGURE 6.—Plots and regressions of batch fecundity (thousands of eggs) versus total length (mm) and weight (kg) for female cabezon from Puget Sound.

March to April. The spawning season reported for *S. marmoratus* in California is half as long (November to March) and peak spawning occurs 3 to 4 months earlier (O'Connell 1953) than found in this study. This is contrary to what one might expect based on general patterns (Qasim 1956). Teleosts in high latitudes generally spawn once and have relatively short spawning seasons during the winter and early spring. On the other hand, most fishes at lower latitudes have protracted spawning seasons and spawn more than once. Seasonal fluctuations in production cycles (food supply) are less defined in lower latitudes, hence females are able to feed more or less continuously to build sufficient energy reserves for a longer spawning season consisting of multiple batches. Spawning time and duration usually synchronize with production cycles so that larvae have a better chance for survival (Nikolsky 1963; Cushing 1982).

Female cabezon are probably similar to other species of marine sculpins along the west coast which spawn multiple batches of eggs during a single spawning season (Atkinson 1939; DeMartini 1978; Goldberg 1980). O'Connell (1953) suspected

that cabezon in California spawned more than once. Evidence from this study also strongly suggests that sexually mature female cabezon spawn more than once during a single spawning season. Species with protracted spawning seasons characteristically spawn more than once per season compared with species with relatively short spawning seasons which spawn only once (Qasim 1956).

Another strong indication of multiple spawning is the presence of two distinct modes of yolked oocytes in ovaries. A second mode was present both in females about to spawn, and in females which had spawned at least once. An intermediate mode consisting of vitellogenic oocytes suggests that females are capable of spawning more than once in a single season (Goldberg 1981). It does not appear that the intermediate generation of yolked eggs are retained for the following season, because cabezon ovaries undergo resorption in the fall (Stage VIII) prior to beginning another cycle the following season (Stage I; Fig. 3I).

Interestingly, after March 1985, all females captured had spawned at least once. The ovaries of all females captured between March and September were either in the process of bringing another batch of eggs to maturity, or in the process of resorption. Multiple spawning is a possible explanation for the absence of females with ovaries in the unspawned condition during the March to September period.

Multiple spawning is also a logical explanation for the relatively low WGSI value for cabezon ovaries with yolked and unhydrated eggs (Stage III). Gunderson and Dygert (1988) showed a relation between "reproductive effort" (WGSI) and natural mortality (M) in numerous species of marine fish ($r^2 = 0.81$). The higher the natural mortality (M), the shorter the longevity ($t_{0.01}$) of the species and thus the greater the "reproductive effort" invested in any given year. The two extremes cited were the northern anchovy ($M = 0.92$, $t_{0.01} = 6$ years, WGSI = 0.65) and dogfish ($M = 0.09$, $t_{0.01} = 57$ years, WGSI = 0.04). Since few cabezon probably live past 20 years (O'Connell 1953; Lauth 1987), one would expect their respective WGSI to fall somewhere between the northern anchovy and dogfish. The very low cabezon WGSI is therefore consistent with multiple spawning, since it should theoretically be higher than dogfish, which it is, but only if multiple spawning is taken into consideration.

Batch fecundities predicted from regressions on weight and length ranged between 66,000 and 152,000 eggs for females from 2.5 kg to 10.5 kg and between 57,000 and 137,000 eggs for females from 500 mm to 775 mm. O'Connell (1953) also found a linear relationship between total weight of females and batch fecundity. Batch fecundities for cabezon greater than 2.7 kg were slightly higher for combined unspawned and spawned females from California and ranged from 48,700 to 96,700 eggs for females between 1.4 kg and 4.6 kg (O'Connell 1953).

Of course, total fecundity of cabezon depends on spawning frequency. The number of times a female actually spawns may depend on a host of biotic and abiotic factors such as food availability and water temperature. The intermediate mode may represent a reserve of eggs that a female can spawn within a single season. The actual number of times a female spawns and the number of eggs released each time, however, may ultimately depend on the amount of energy allotted for reproduction given the prevailing physical and biological conditions. In smaller females, more of the energy would be utilized for growth or basic metabolic needs, hence, less energy would be available for egg production.

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SEASONAL COMPOSITION AND ABUNDANCE OF DECAPOD AND STOMATOPOD CRUSTACEANS FROM COASTAL HABITATS, SOUTHEASTERN UNITED STATES[1]

ELIZABETH L. WENNER AND CHARLES A. WENNER[2]

ABSTRACT

Decapod and stomatopod crustaceans were collected by trawl during seasonal cruises from Cape Fear, North Carolina to Cape Canaveral, Florida at depths from 4 to 20 m. A total of 60 species of decapod and 3 species of stomatopod crustaceans were collected. Fifteen species accounted for 95% of the total number of individuals and 96% of the total biomass: the portunid crabs *Portunus gibbesii, P. spinimanus, Ovalipes stephensoni, O. ocellatus, Callinectes similis, C. sapidus,* and *Arenaeus cribrarius*; the calappid crab *Hepatus ephelitius*; the majid crab *Libinia emarginata*; the penaeid shrimps *Penaeus setiferus, P. aztecus, P. duorarum,* and *Trachypenaeus constrictus*; and the squillid stomatopods *Squilla empusa* and *S. neglecta.*

Season was an important factor affecting the number of individuals and species collected during the study. No consistent changes in number of species, total number of individuals, and mean total weight occurred with latitude. Cluster analysis indicated season and latitude were important factors determining species assemblages in the coastal zone. Although changes in species composition occur seasonally, most species groups delineated by cluster analysis were not consistently collected nor restricted to particular site groups. A seasonally ubiquitous faunal assemblage in the coastal zone was composed of numerically dominant species. Those assemblages which were characterized as being restricted to site groups consisted of relatively rare species or those which were associated with hard-bottom habitat.

Integrated community analyses of the decapod Crustacea of the Carolinean shelf province, extending from Cape Fear, NC to Cape Canaveral, FL were completed by Wenner and Read (1981, 1982). Their studies, which encompassed a broad latitudinal and bathymetric range, described assemblages of decapod Crustacea from the continental shelf of the southeastern United States in terms of depth, season, and latitude and provided estimates of decapod abundance relative to certain biological and physical factors. Although Wenner and Read (1981, 1982) sampled the continental shelf habitats described by Struhsaker (1969), their effort in coastal habitats was limited to depths of 9–18 m.

The coastal zone, defined by Struhsaker (1969) as extending from the sounds and estuaries out to depths of 18 m, has been extensively surveyed since the 1930's (Keiser 1977); however, most of the resulting reports described the composition and magnitude of the incidental catch of finfishes by shrimp trawlers (see Keiser 1977 for literature survey). Information on invertebrates, and more specifically the noncommercially important species of decapod and stomatopod crustaceans, has been limited. Hoese (1973) reported on the seasonal distribution of decapod and stomatopod species collected on the central Georgia coastal zone and Doboy Sound. Keiser (1977) identified 20 species of decapod and stomatopod crustaceans in a study of the incidental catch of the South Carolina shrimp fishery. Anderson et al. (1977) provided seasonal information on 12 species of decapod and stomatopod crustaceans collected during a survey of the macrofauna in the surf zone off Folly Beach, SC. The present paper describes the assemblages of decapod and stomatopod crustaceans in coastal habitats off the southeastern United States in terms of seasonal and latitudinal variations and characterizes the important species in terms of their abundance, biomass, size composition, and distribution.

METHODS AND MATERIALS

Data Collection

Samples of decapod and stomatopod Crustacea were collected during seasonal cruises from Cape Fear, NC (lat. 33.9°N) to Cape Canaveral, FL (lat.

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28.5°N) at depths ranging from 4 to 20 m. Dates of the four seasonal cruises were as follows: summer, 15 July–20 September 1980; spring, 28 April–6 June 1981; winter, 7–29 January 1982; fall, 14 October–7 December 1982. Sampling locations were selected by means of a stratified random sampling design (Grosslein 1969). Thirteen strata were established at depths of 4–12 m from Cape Fear to the mouth of the St. John's River, FL (lat. 30.4°N), while south of this point to Cape Canaveral, an additional five strata were delineated in depths ranging from 8 to 20 m with the 5.6 km territorial sea line as the offshore boundary. A change in definition of strata off Florida was necessary because of the steepness of the nearshore continental shelf in the area south of the St. John's River. Areal extent of strata ranged from 7,486 to 31,661 ha ($\bar{x}$ = 17,323 ha).

At each randomly selected site within a stratum, paired tows were made for 20 minutes at a speed of 4.4 km/h using four-seam Gulf of Mexico shrimp trawl nets. Outriggers enabled two nets to be fished simultaneously from the same vessel. The trawl nets, which were attached to 1.5 × 0.8 m wood and chain doors, had headrope lengths of 12.8 m, footrope lengths of 15.8 m and stretch-mesh sizes of 5.1 cm in the wings, 4.4 cm in the body, and 4.1 cm in the cod end. Tickler chains were attached to each door and adjusted to drag at a distance of 0.6 m in front of the nets. Tows were confined to daylight hours (1 hour after sunrise to 1 hour before sunset) to eliminate day-night changes in availability and vulnerability of organisms to the gear. Sampling effort changed from cruise to cruise owing to constraints of funding and vessel availability (Fig. 1). Collections of decapod and stomatopod crustaceans taken during tows in which a net was damaged, failed to reach bottom, or became twisted were considered unsuccessful and were not included in analyses. Bottom temperature was measured following each tow with a stem thermometer mounted within a Van Dohrn bottle.

Decapod and stomatopod crustaceans collected by each net during a tow were identified to species, counted, and weighed to the nearest gram, and either the entire catch or a random subsample of at least 30 individuals was measured to the nearest mm. Measurements included total length (tip of rostrum to tip of telson) for shrimp [carapace length (tip of rostrum to posterior margin of carapace) for majid crabs, and carapace width (measured between the posteriormost lateral spines) for other crabs]. Sex was recorded for brachyuran species. Although the contents of each net were processed independently, the catch per standard tow is defined as the combined catch from both trawl nets fished simultaneously at each randomly chosen site within a stratum.

Data Analysis

The stratified mean catch per tow and its standard error were calculated by the expressions (Poole 1974):

$$\bar{y}_{ST} = \sum_{h=1}^{L} \frac{N_h \bar{y}_h}{N}$$

$$SE_{\bar{y}_{ST}} = \left[\sum W_h^2 \cdot \frac{s_h^2}{n_h} \left(1 - \frac{n_h}{N_h} \right) \right]^{1/2}$$

where $\bar{y}_{ST}$ = stratified mean catch/tow
$\bar{y}_h$ = mean catch/tow in numbers or weight in the h stratum
N_h = number of possible sampling units in the h stratum
N = total number of possible sampling units over all strata
$SE_{\bar{y}_{ST}}$ = standard error of the stratified mean catch/tow
W_h = N_h/N
S_h^2 = sample variance of the h stratum
n_h = number of trawl tows made in the h stratum.

The effective degrees of freedom for the calculation of confidence limits follows the methodology of Cochran (1977).

Minimum biomass and density estimates for trawl-caught groundfish were calculated from computations of the area swept by the trawl gear. The approximation of the area swept (a) was derived from the following equation (Roe 1969):

$$a = \frac{K \times M \times (0.6\ H)}{10{,}000\ \text{m}^2/\text{ha}}$$

where a = swept area in hectares
K = speed in meters per hour
M = time in hours fished
H = headrope length in meters.

The result (1.12 ha) was multiplied by two since the standard unit of effort was two nets fished simultaneously. Thus, a standard trawl station sampled 2.24 ha.

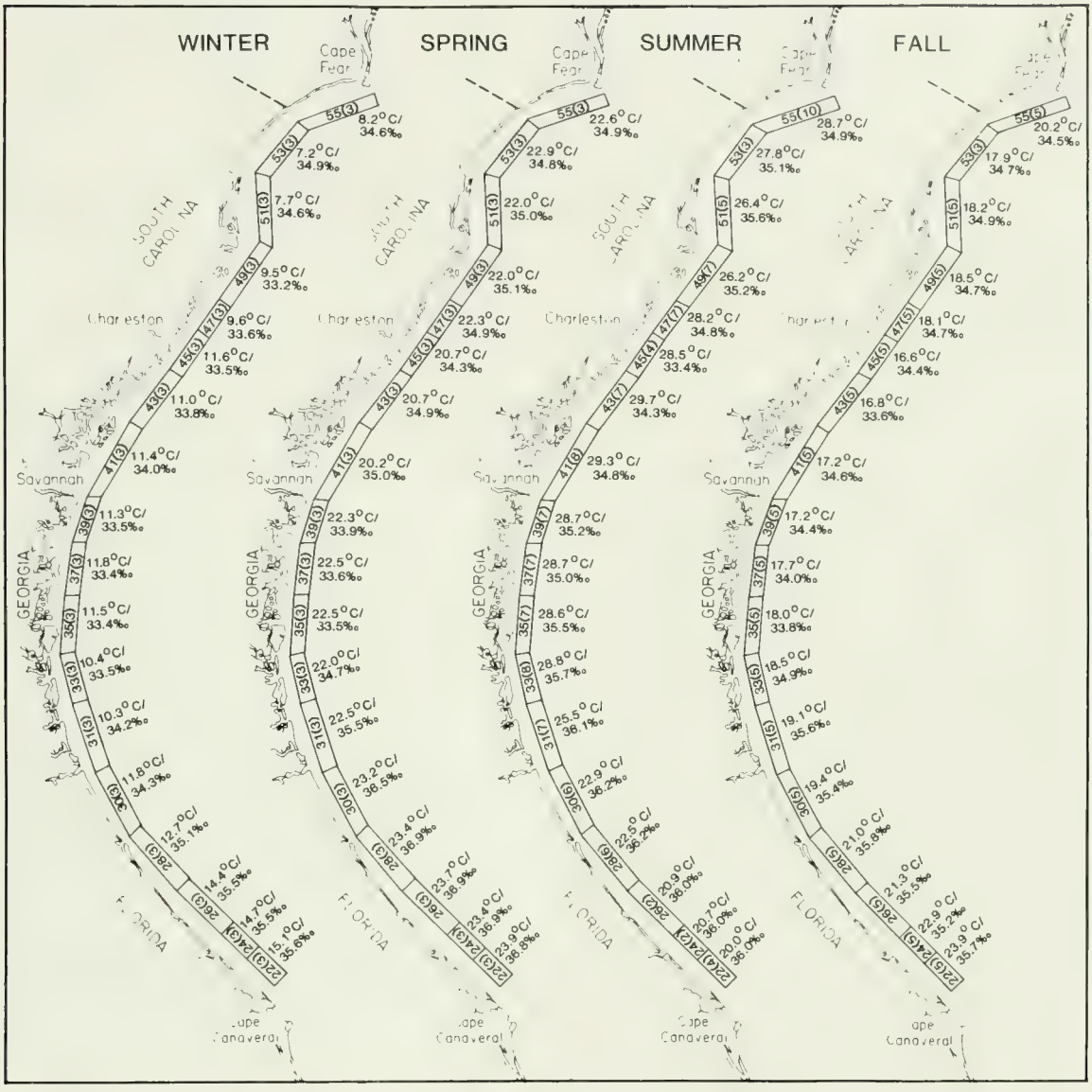


FIGURE 1.—Location and number of collections (in parentheses) from each stratum during seasonal sampling periods. Average temperature and salinity conditions during sampling are noted for each stratum.

Statistically significant differences in biomass, number of species, and number of individuals between seasons were determined by the Kruskal-Wallis analysis of variance by ranks (Zar 1984). This nonparametric equivalent of analysis of variance was used because a logarithmic transformation failed to normalize the data. The nonparametric analog of the Tukey multiple comparison test (Zar 1984) was used following rejection of the null hypothesis to determine between which of the samples significant differences occurred. The rejection level for the null hypothesis in all statistical tests was $\alpha = 0.05$.

Cluster analysis was used to determine seasonal patterns of similarity among strata and to define assemblages of decapod and stomatopod crustaceans. Prior to analysis, data from standard tows during a season were pooled within each stratum. Data were reduced to eliminate species which occurred in only one stratum during all seasons. The rationale to exclude these species was that they did

not appear to be habitat-restricted, nor did they exhibit a meaningful distribution pattern (Clifford and Stephenson 1975), as indicated by the tendency of the entities to chain rather than form new groups.

Species and pooled collections from a stratum were classified using flexible sorting (Lance and Williams 1967) with a cluster intensity coefficient (β) of -0.25. The similarity coefficient used was the Bray-Curtis measure (Clifford and Stephenson 1975) on percent standardized data (Boesch 1977).

The postclustering technique of nodal analysis (Williams and Lambert 1961; Lambert and Williams 1962) was used to describe site groups in terms of their characteristic species and species groups in terms of their occurrence within site groups. Nodal analysis interpretations were made by using patterns of constancy (a measure of how consistently a species is found in a site group) and fidelity (a measure of how restricted a species group is to a site group). Mathematical definitions of constancy and fidelity and a more detailed explanation of cluster and nodal analysis are found in Boesch (1977).

RESULTS AND DISCUSSION

Hydrographic Measurements and Description of the Study Area

The coastal zone as defined by Struhsaker (1969) ranges from the beaches to 16–24 km offshore where the water depth is 9–18 m. The sea bottom within this depth zone is mostly homogeneous in composition, consisting predominantly of sandy mud with varying amounts of ground-shell. The bottom is ripple-marked by wave action to a depth of 20 m (Sandifer et al. 1980). Hard or "live" bottom reefs are interspersed throughout the coastal zone (Buchanan 1973) and are distinguished from the surrounding sand biotope by supporting a diverse assemblage of sessile invertebrates as well as numerous motile species which are inhabitants of the complex microhabitats (e.g., rock crevices, bare rock, ledges with sand veneer, sand patches between rocks, and sessile organisms) of the reefs (Wenner et al. 1983).

The hydrography of the coastal zone has not been studied as thoroughly as other areas of the continental shelf. The interacting forces of river runoff, wind direction and force, seasonal air temperatures, and proximity of the Gulf Stream produce complicated patterns of circulation (Bumpus 1973) that determine the distribution of sediments, nutrients, oxygen, temperature, salinity, food, and planktonic forms of larval and adult organisms (Johnson et al. 1974). Bumpus (1973) observed that the southerly flowing coastal current is very transient and restricted to a narrow band along the coast.

Nearshore surface and bottom waters off the southeastern United States have large seasonal variations in temperature. Because of the shallowness of the coastal zone, cooling and warming can occur rapidly when appropriate atmospheric conditions exist; when the amount of cold, fresh, runoff is variable; or when the movement of the Gulf Stream is variable (Mathews and Pashuk 1984). A well-defined recurrent seasonal upwelling exists off the coast of Florida near Cape Canaveral, which occurs in late July with anomalously low multiyear monthly mean surface temperatures (Smith 1983; Lee and Pietrafesa 1987). Warming of bottom waters usually occurs in late August.

Mean bottom water temperatures for each stratum during the present study increased with decreasing latitude for every sampling period except summer (Fig. 1). During that time, temperatures ranging from 20.0° to 23.1°C were noted off the coast of Florida, while the extremes recorded for strata off North Carolina, South Carolina, and Georgia were 25.5°–29.7°C. Temperature extremes during the other sampling periods varied predictably with latitude. During winter sampling, temperatures ranged from a low of 7.2°C off North Carolina to 15.1°C at the southernmost stratum off Florida. Temperatures in spring were the least variable with regional extremes of 20.2°–23.9°C noted. The lowest temperatures were recorded in strata between Charleston, SC and Savannah, GA. Temperatures during the fall sampling ranged from 16.6° to 23.9°C, with the lowest temperatures again occurring for strata between Charleston and Savannah.

Salinity of nearshore waters is generally lower than that of the open shelf because of runoff from rivers. Blanton and Atkinson (1978) noted that runoff into the coastal zone is bimodal with a major peak in spring and a minor peak in late summer. Because most of the freshwater on the open shelf is confined to depths <20 m, salinity regimes 10 or 20 km off the Georgia coast are similar to those of a partially mixed estuary. Rapid mixing occurs due to large tidal fluxes (Blanton and Atkinson 1978). Salinities of bottom waters measured during the present study were fairly uniform seasonally. Highest values were noted for coastal waters off the coast of Florida, while lowest salinities occurred off South Carolina and Georgia (Fig. 1).

Species Composition

A total of 60 species of decapod and 3 species of stomatopod crustaceans comprising 59,966 individuals and 11,000 individuals, respectively, was collected during the study (Table 1). Fifteen species accounted for 95% of the total number and 96% of the total biomass: the portunid crabs *Portunus gibbesii, P. spinimanus, Ovalipes stephensoni, O. ocellatus, Callinectes similis, C. sapidus,* and *Arenaeus cribrarius*; the calappid crab *Hepatus epheliticus*; the majid crab *Libinia emarginata*; the penaeid shrimps *Penaeus setiferus, P. aztecus, P. duorarum,* and *Trachypenaeus constrictus*; and the squillid stomatopods *Squilla empusa* and *S. neglecta.* The ranking of these species in terms of numbers of individuals and biomass changed seasonally; however, *Portunus gibbesii* was the most abundant species collected during all seasons except spring, when *Ovalipes stephensoni* dominated catches (Table 1). Previous faunal surveys in the Carolinian Province have shown that *P. gibbesii* is a common and abundant inhabitant of the coastal zone (Hay and Shore 1918; Wass 1955; Rouse 1970). Published information on *O. stephensoni* is limited, but it has previously been reported (as *O. quadulpensis*) by Hoese (1973) not to be common in trawl catches off Georgia. Biomass of catches was dominated by *Callinectus sapidus* during all seasons except fall when *Penaeus setiferus* ranked first. Keiser (1976) likewise noted that *C. sapidus* comprised a large portion by weight of the incidental invertebrate catch of the shrimp fishery off South Carolina. The importance of *P. setiferus* in catches during the fall is not unexpected since the species forms the basis of a major commercial fishery in the South Atlantic Bight during that time (Keiser 1976, 1977).

Community, Biomass, and Density Estimates

Season was an important factor affecting the number of individuals and species collected during the study (Table 2). The median number of individuals was significantly less during winter sampling than at other seasons ($\chi^2 = 29.83$, $P < 0.001$), while the median number of species was significantly less during winter and spring ($\chi^2 = 45.60$, $P < 0.001$). Stratified mean catch per tow values also reflected seasonal differences with considerably fewer individuals and lower biomass in catches during winter (Table 3). Similarly, mean total biomass (kg/ha) and density (no./ha) estimates were lowest for winter. No consistent changes in number of species or number of individuals occurred with latitude (Table 2); however, the number of individuals was consistently low at stratum 22 off Cape Canaveral.

Our results suggest that the community structure of decapod and stomatopod crustaceans from the coastal zone is influenced primarily by seasonality and not latitude. Other investigators have likewise noted the influence of seasonality on the number of motile invertebrate species in inshore habitats. Van Dolah et al. (1984) found that the median number of invertebrate species collected by trawl off the mouth of Winyah Bay, SC was greater in summer than winter. Anderson et al. (1977) collected more species of fishes and invertebrates in the surf zone in summer than any other season, with diversity being least in winter. These results are not surprising since the coastal region of the southwestern Atlantic is prone to great seasonal changes in water temperature. The occurrence of more species, more individuals, and greater biomass in summer may result from more uniform temperatures across the entire shelf allowing intrusion into the coastal zone by middle- and outer-shelf species which represent a northern extension of the tropical Gulf of Mexico and Caribbean fauna (Cerame-Vivas and Grey 1966), as well as offshore movement by euryhaline estuarine species. The modifying influence of currents, river runoff, and air temperature tend to obscure any latitudinal gradients in community structure. Briggs (1974) considered Cape Canaveral as a zoogeographic boundary for inner-shelf fauna since many species terminated their range there; however, he hastened to point out that Cape Canaveral is an intermediate point in a lengthy geographic area of change. Depending on water temperature, eurythermic tropical species can extend far north in the Carolinean Province. During winter under strong northeasterly winds, an inshore zone of cold Virginian coastal current extends south of Cape Hatteras enabling intrusion by northern temperate species (Cerame-Vivas and Grey 1966). Latitudinal trends in community structure are further obscured by using quarterly data to show relationships and the tendency of many species which inhabit the inner shelf on a regular basis to have broad latitudinal ranges.

The coastal zone along the southeastern United States has previously been reported to contain few species of decapod crustaceans with high abundance (Wenner and Read 1981, 1982). The low number of species in the coastal zone was attributed to the more rigorous and variable hydrographic conditions coupled with a relatively homogeneous substrate compared with other areas of the continental shelf.

TABLE 1.—Decapod and stomatopod crustaceans collected in the coastal zone between Cape Fear, NC and Cape Canaveral, FL. Species are ranked according to numerical abundance. Numbers listed under seasons show rank by number and biomass (in parentheses) during each season, while (+) indicates occurrence.

Species	Number station occurrences	Total number specimens	Total biomass (kg)	Seasonal ranking			
				W	Sp	Su	Fa
Portunus gibbesii	273	17,250	115.2	1(5)	2(3)	1(9)	1(3)
Squilla empusa	237	9,112	137.5	2(4)	3(4)	3(4)	4(4)
Ovalipes stephensoni	155	8,641	56.7	6(7)	1(2)	6(11)	11(13)
Callinectes similis	194	6,470	125.4	14(10)	11(12)	4(3)	2(2)
Penaeus setiferus	192	5,516	133.7	3(3)	15(14)	5(5)	3(1)
Penaeus aztecus	155	4,622	74.4	+	+	2(2)	(15)
Portunus spinimanus	221	2,913	52.1	8(6)	5(7)	7(10)	6(8)
Ovalipes ocellatus	163	2,523	73.9	11(8)	4(5)	9(6)	10(9)
Hepatus epheliticus	197	2,332	77.8	15(14)	10(8)	8(7)	5(5)
Squilla neglecta	150	1,887	21.7	+	6(10)	12(13)	9(12)
Callinectes sapidus	173	1,577	253.3	7(1)	9(1)	10(1)	(6)
Arenaeus cribrarius	130	1,510	57.8	(13)	13(11)	11(8)	8(7)
Trachypenaeus constrictus	118	1,025	3.1	4(9)	14	+	7
Libinia emarginata	170	1,008	50.7	5(2)	8(6)	(12)	(10)
Penaeus duorarum	101	858	12.2	+	7(9)	+	+
Pagurus pollicaris	159	795	1.3	13	+	14	15
Callinectes ornatus	90	788	10.8	+		13(14)	13(14)
Libinia dubia	151	575	10.3	9(12)	+	+	12(11)
Persephona mediterranea	149	567	8.2	+	12(15)	15(15)	+
Xiphopenaeus kroyeri	20	346	1.7	10		+	14
Porcellana sigsbeiana	25	99	0.1	+	+	+	
Cancer irroratus	25	81	0.9	12(11)	+	+	+
Neopanope sayi	30	66	0.1	+	+	+	+
Menippe mercenaria	42	60	8.2	(15)	+	+	+
Sicyonia brevirostris	33	53	0.3		+	+	+
Pagurus annulipes	2	36	—			+	
Pilumnus sayi	19	36	0.1	+	+	+	+
Calappa flammea	21	30	4.3	+	(13)	+	+
Exhippolysmata oplophoroides	9	25	<0.1				+
Pagurus longicarpus	20	25	—	+	+	+	+
Porcellana sayana	16	21	<0.1				+
Hexapanopeus angustifrons	8	11	<0.1	+		+	+
Podochela riisei	10	10	<0.1	+	+	+	
Pagurus hendersoni	1	10	—	+			
Portunus sayi	3	9	<0.1				+
Albunea paretii	5	8	<0.1			+	+
Panopeus occidentalis	5	7	<0.1			+	
Pagurus impressus	5	6	—			+	+
Podochela sidneyi	3	6	<0.1	+		+	
Petrochirus diogenes	4	5	<0.1			+	+
Speocarcinus carolinensis	5	5	0.2			+	+
Sicyonia dorsalis	1	4	<0.1			+	
Synalpheus townsendi	1	4	—			+	
Lysmata wurdemanni	3	4	<0.1	+		+	+
Hypoconcha sabulosa	2	3	<0.1			+	+
Calappa sulcata	3	3	0.3		+		+
Metoporhaphis calcarata	3	3	<0.1	+			+
Dromidia antillensis	2	2	<0.1			+	
Pilumnus dasypodus	2	2	<0.1			+	+
Euryplax nitida	1	2	<0.1	+			
Pinnixa chaetopterana	1	2	<0.1				+
Hepatus pudibundus	2	2	<0.1			+	+
Sicyonia typica	1	1	<0.1		+		
Polyonyx gibbesi	1	1	<0.1				+
Calappa angusta	1	1	<0.1			+	
Calappa ocellata	1	1	<0.1			+	
Pinnotheres maculatus	1	1	—	+			
Pinnixa cylindrica	1	1	<0.1			+	
Pelia mutica	1	1	<0.1			+	
Mithrax pleuracanthus	1	1	<0.1			+	
Parthenope serrata	1	1	<0.1			+	
Dardanus fucosus	1	1	—				+
Lysiosquilla scabricauda	1	1	<0.1				+

TABLE 2.—Number of individuals (N) and number of species (S) for pooled replicate samples of invertebrates at each station.

	Winter		Spring		Summer		Fall	
Strata	N	S	N	S	N	S	N	S
22	43	13	207	18	319	26	238	21
24	78	13	553	17	425	19	1,608	25
26	72	11	526	15	787	20	1,376	27
28	1,707	19	1,074	15	1,301	23	1,823	22
30	172	13	373	17	2,199	25	1,609	22
31	370	21	1,580	20	2,037	24	1,849	23
33	900	15	1,961	17	1,313	20	513	17
35	9	3	609	17	2,688	26	3,071	24
37	399	12	592	15	1,648	26	458	21
39	196	17	1,207	18	1,178	23	592	19
41	51	15	934	15	399	24	232	16
43	264	14	349	15	791	18	2,082	23
45	149	15	1,506	21	1,780	16	1,843	22
47	71	16	214	14	1,269	24	1,053	23
49	213	18	1,658	19	3,235	25	1,417	24
51	70	11	266	15	1,308	25	804	21
53	22	11	1,673	16	1,534	21	616	22
55	177	16	1,927	16	2,906	22	892	22

TABLE 3.—Seasonal stratified mean catch per tow for total number and weight of decapod and stomatopod crustaceans, and density estimates based on a swept area of 2.24 hectares during a standard station.

	Stratified mean catch/tow		Mean	Mean
Season	No. of individuals	Biomass	density No./ha	biomass kg/ha
Winter	99	1.969	44	0.879
Spring	298	4.491	133	2.005
Summer	277	5.666	124	2.529
Fall	248	4.283	111	1.912

Hoese (1973) attributed a higher density and biomass of invertebrates in Doboy Sound than in inshore and offshore areas of Georgia to a proximity to productive salt marsh. Comparisons of study results with biomass and density estimates obtained for decapod crustaceans from high salinity areas sampled in Charleston Harbor, SC (Wenner et al. 1984) support Hoese's findings of a decrease in biomass and density from estuarine to nearshore habitats.

Species Assemblages and Distributional Patterns

Normal cluster analysis classified pooled collections from each stratum into seven groups which corresponded to season of collection and latitudinal location (Fig. 2). Within each of two major groupings of the dendrogram (Groups 1–4 and Groups 5–7), latitudinal-related groups occurred seasonally. Group 1 contained collections having similar faunal composition which were primarily off South Carolina and Georgia during spring. Collections in this group were least similar faunistically to those in groups 2–4. Collections in group 2 were also faunistically distinct and were mainly taken off Florida and South Carolina in fall. Group 3 represented a highly similar latitudinal grouping of collections with most taken off Georgia during fall and winter. This group contained collections that were similar in species composition to those in group 4. Group 5 was least similar to groups 5–6 and contained collections from Georgia, Florida, and South Carolina from fall, spring, and summer. Collections in group 6 were from all locations but were taken only in summer and fall. Some latitudinal grouping of collections was evident in group 7 which mostly contained those off Florida.

The species assemblages identified by inverse cluster analysis (Table 4) displayed generally low constancy for site groups, except for Groups A and B which contained the numerically dominant decapod species. Species in these groups had moderate to high constancy for all site groups and, consequently, were not restricted to any group (Fig. 3).

TABLE 4.—Species groups resulting from inverse cluster analysis using the Bray-Curtis similarity coefficient and flexible sorting.

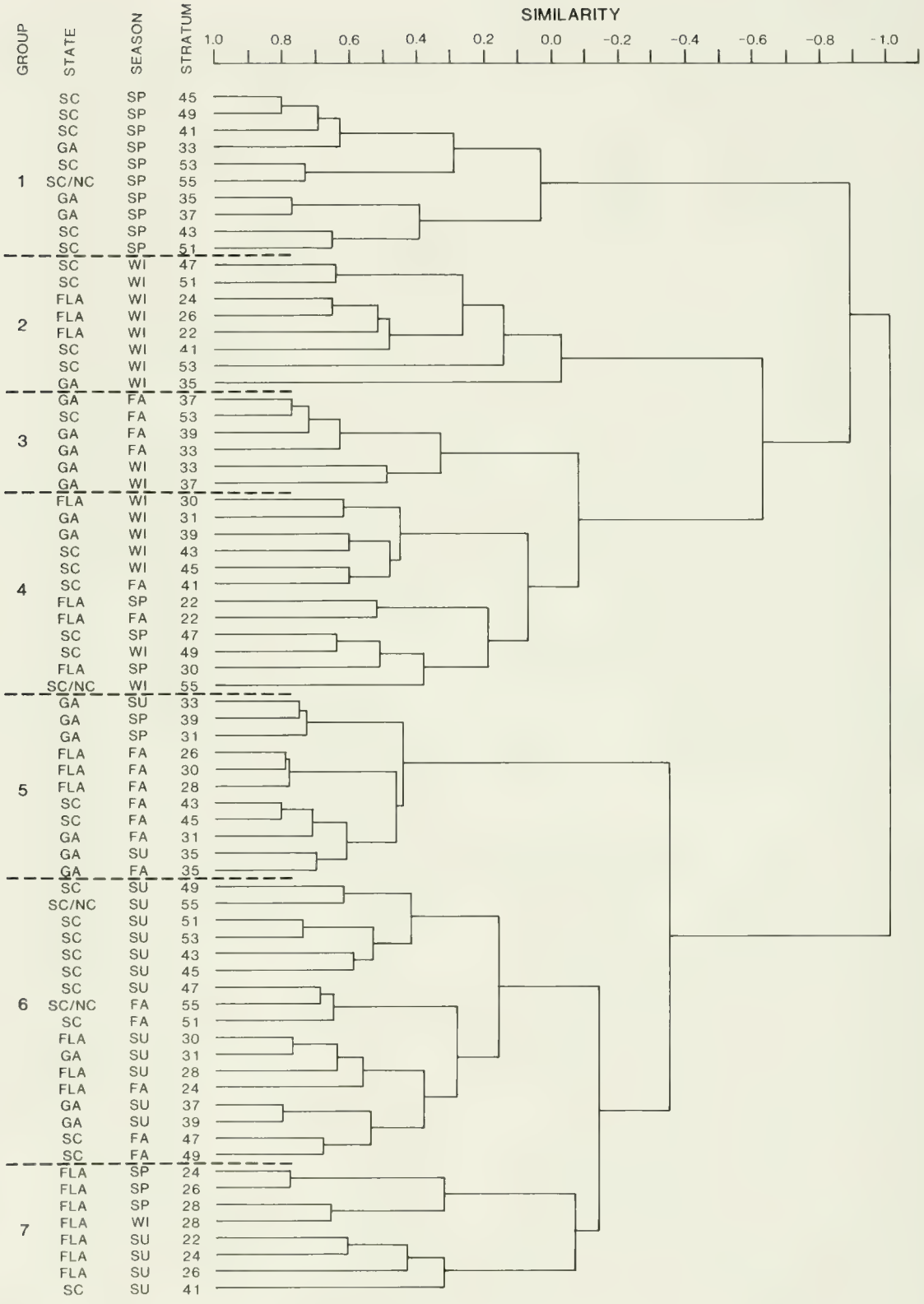
Group A
- *Portunus gibbesii*
- *Squilla empusa*
- *Penaeus setiferus*
- *Penaeus duorarum*
- *Trachypenaeus constrictus*
- *Ovalipes stephensoni*
- *Ovalipes ocellatus*
- *Squilla neglecta*
- *Callinectes sapidus*
- *Pagurus pollicaris*
- *Persephona mediterranea*
- *Hepatus epheliticus*
- *Portunus spinimanus*
- *Libinia emarginata*
- *Libinia dubia*
- *Penaeus aztecus*
- *Callinectes similis*
- *Arenaeus cribrarius*
- *Callinectes ornatus*

Group B
- *Exhippolysmata oplophoroides*
- *Porcellana sayana*
- *Xiphopenaeus kroyeri*

Group C
- *Albunea paretii*
- *Hepatus pudibundus*
- *Petrochirus diogenes*
- *Speocarcinus carolinensis*
- *Portunus sayi*
- *Pagurus impressus*
- *Calappa sulcata*

Group D
- *Dromidia antillensis*
- *Panopeus occidentalis*
- *Hypoconcha sabulosa*
- *Podochela sidneyi*

Group E
- *Pilumnus dasypodus*
- *Metoporhaphis calcarata*
- *Pilumnus sayi*
- *Neopanope sayi*
- *Podochela riisei*
- *Pagurus longicarpus*
- *Hexapanopeus angustifrons*
- *Cancer irroratus*
- *Sicyonia brevirostris*
- *Menippe mercenaria*
- *Porcellana sigsbeiana*
- *Calappa flammea*
- *Lysmata wurdemanni*


SIMILARITY
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
GROUP
STATE
SEASON
STRATUM
1
SC SP 45
SC SP 49
SC SP 41
GA SP 33
SC SP 53
SC/NC SP 55
GA SP 35
GA SP 37
SC SP 43
SC SP 51
2
SC WI 47
SC WI 51
FLA WI 24
FLA WI 26
FLA WI 22
SC WI 41
SC WI 53
GA WI 35
3
GA FA 37
SC FA 53
GA FA 39
GA FA 33
GA WI 33
GA WI 37
4
FLA WI 30
GA WI 31
GA WI 39
SC WI 43
SC WI 45
SC FA 41
FLA SP 22
FLA FA 22
SC SP 47
SC WI 49
FLA SP 30
SC/NC WI 55
5
GA SU 33
GA SP 39
GA SP 31
FLA FA 26
FLA FA 30
FLA FA 28
SC FA 43
SC FA 45
GA FA 31
GA SU 35
GA FA 35
6
SC SU 49
SC/NC SU 55
SC SU 51
SC SU 53
SC SU 43
SC SU 45
SC SU 47
SC/NC FA 55
SC FA 51
FLA SU 30
GA SU 31
FLA SU 28
FLA FA 24
GA SU 37
GA SU 39
SC FA 47
SC FA 49
7
FLA SP 24
FLA SP 26
FLA SP 28
FLA WI 28
FLA SU 22
FLA SU 24
FLA SU 26
SC SU 41

Wenner and Read (1982) found that *Trachypenaeus constrictus*, *Portunus spinimanus*, *P. gibbesii*, and *Ovalipes stephensoni* form a frequently co-occurring assemblage on the inner shelf. Although their importance in terms of abundance and biomass changed seasonally, all species in groups A and B, except *Callinectes ornatus*, were collected during every sampling period, indicating that these species are a core-assemblage of the coastal zone. Several species in these groups (*O. ocellatus*, *P. gibbesii*, and *P. spinimanus*) are common inhabitants of high-salinity estuarine waters in South Carolina (Wenner et al. 1984) and Georgia (Hoese 1973), while others, such as *C. sapidus*, *Penaeus setiferus*, and *P. aztecus*, are migratory and seasonally dominant inhabitants of estuarine systems in the southeastern United States (Weinstein 1979; Wenner et al. 1983, 1984). Another member of this assemblage, *Arenaeus cribrarius*, is a common member of the sandy beach community along the southeastern United States (Pearse et al. 1942; Williams 1984; Anderson et al. 1977; Leber 1982; DeLancey 1984).

Species from groups C and D were restricted to sites as indicated by moderate to high fidelity values and have previously been reported as nearshore inhabitants of the southwestern Atlantic (Williams 1984). Most species in these groups are found on sand or mud bottom and occur throughout the latitudinal extent of the study area (Williams 1984). Exceptions include *Portunus sayi* which is commonly associated with *Sargassum* (Williams 1984), and *Hepatus pudibundus* which has not been reported north of Georgia (Coelho and Ramos 1972). Species in Group E are generally associated with hard-bottom areas (Wenner and Read 1982; Williams 1984) and were neither abundant or commonly encountered in the coastal habitat. These species were most restricted in their distribution to collections from site group 7.

Group E contained species which were not constant or faithful to any site groups. In addition, there was no consistency in their occurrence with regard to season, latitude, or substrate preference. Most of the species in this group have broad bathymetric ranges on the continental shelf and none were abundant in our collections from the coastal zone.

Seasonality and latitude are important factors determining species assemblages in coastal habitats. The grouping of strata by season suggests that the decapod and stomatopod fauna of the coastal zone changes throughout the year and may also change with latitude. Although changes in species composition occur seasonally, most species groups delineated by cluster analysis were not consistently collected nor restricted to particular site groups. A seasonally ubiquitous faunal assemblage in the coastal zone was composed of numerically dominant species. The species assemblages which were characterized as being restricted to site groups consisted of relatively rare species or those which were associated with hard-bottom habitat.

FIGURE 2.—Normal cluster dendrogram of site groups formed using percent standardization and flexible sorting. Data from standard tows during a season were pooled within each stratum.

Temporal and Spatial Distributions of Numerically Dominant Species

Portunus gibbesii

Although its known range extends from southern Massachusetts through the Gulf of Mexico, this portunid crab is more common and abundant in shallow shelf waters of the Carolinean Province and Caribbean Sea (Williams 1984). *Portunus gibbesii* has been reported on mud, sand, and shell substrates (Park 1969, 1978).

This species far outranked other decapod and stomatopod crustaceans in total number (24% of the total catch) and was present in 273 of the 303 collections made during all seasons (Table 1). In terms of biomass, *P. gibbesii* was the fifth most important species collected, constituting 9% of the total catch by weight. Abundance differed seasonally, with the stratified mean catch per tow being highest in fall (79 individuals/tow) and lowest in winter (26 individuals/tow) (Table 5). The number of individuals per tow differed between areas with more *P. gibbesii* collected in strata off Georgia during every season (Fig. 4).

The mean size of *P. gibbesii* differed between areas with largest crabs ($\bar{x}$ CW = 50 mm, n = 1,484) caught off Florida. Crabs off Georgia averaged 44 mm CW (n = 2,347), while those from strata off South Carolina/North Carolina averaged 41 mm CW (n = 3,158), suggesting decreased size with increasing latitude. Mean size of *P. gibbesii* differed between seasons, with smallest individuals collected in summer ($\bar{x}$ CW = 37.5 mm, n = 1,985). Mean carapace width of individuals was similar during other seasons (winter: $\bar{x}$ = 46.9 mm, n = 609; spring; ($\bar{x}$ = 48.2 mm, n = 1,305; fall; $\bar{x}$ = 45.9 mm, n = 3,090). Seasonal size differences may reflect influx of crabs from a spring hatch. Ovigerious females occur off Beaufort Inlet, NC from

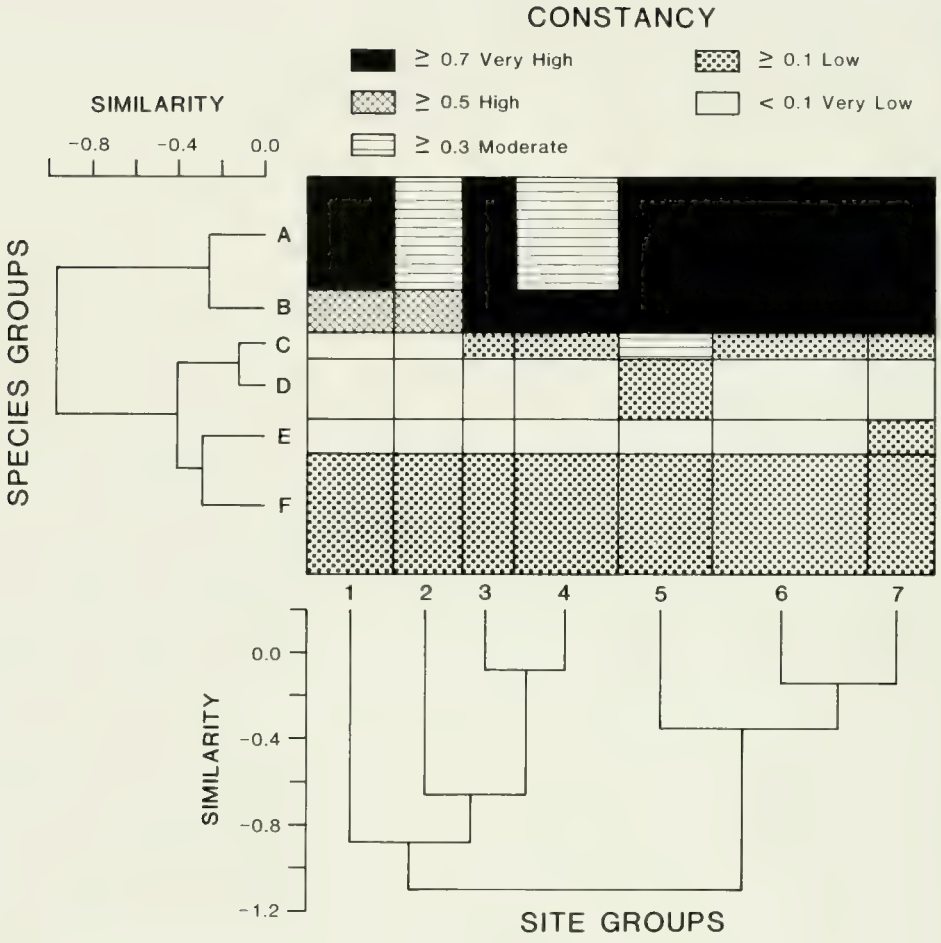


FIGURE 3.—Inverse and normal classification hierarchies and nodal diagram showing constancy and fidelity of site—species group

May to August but are known to occur from February to November in other portions of its range (Dudley and Judy 1961). In the present study, 185 of the 187 ovigerous females collected were taken in spring.

Male *P. gibbesii* were slightly larger ($\bar{x}$ CW = 45.2 mm) than females ($\bar{x}$ CW = 43.2 mm) but were less numerous. Analysis of sex ratios indicated significantly more female crabs than males were collected each season (Table 6).

Squilla empusa

This stomatopod is widely distributed in the western Atlantic, occurring from Maine to South America as far south as Surinam (Manning 1969; Gore and Becker 1976). Camp (1973) found *S. empusa* to be most abundant at 18 m depths on the central west Florida shelf.

This species was the most abundant stomatopod collected and ranked second among the total catch of decapod and stomatopod species. It was frequently collected throughout the study area, occurring in 78% of the 303 trawl tows made. In terms of biomass, *S. empusa* constituted 11% of the total catch, being outranked only by the blue crab, *Callinectes sapidus* (Table 1). The stratified mean catch per tow was highest in spring (40 individuals/tow) and summer (42 individuals/tow) (Table 5). The number of individuals per tow differed between the areas with more *S. empusa* collected off Florida during every season (Fig. 4).

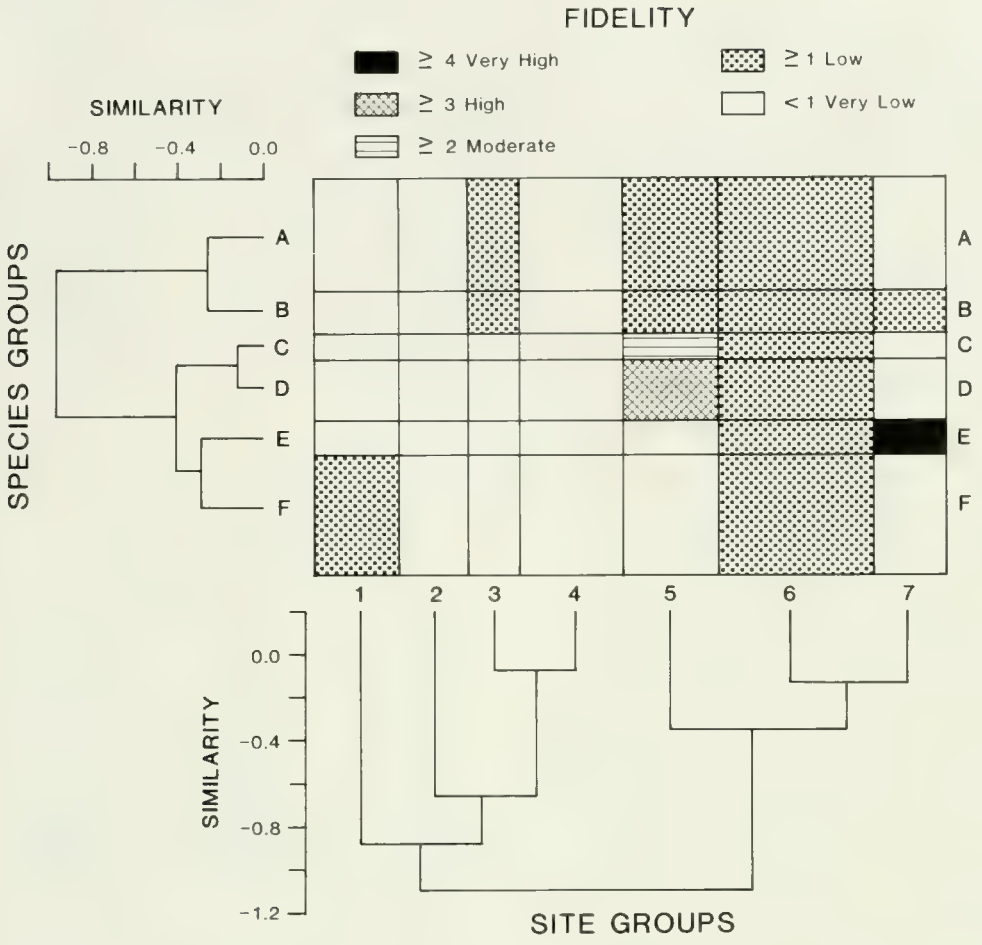


FIGURE 3.—*Continued*—coincidence from pooling collections during a season within each stratum.

Ovalipes stephensoni

This portunid crab, which was the third most abundant species collected in this study (12% of total catch), occurs off Virginia (Musick and McEachran 1972) to near Biscayne Bay, FL (Park 1969). Adult *O. stephensoni* are found farther from shore than adults of its congener *O. ocellatus*; however, young of both species occur nearshore (Williams 1984). Wenner and Read (1982) found *O. stephensoni* to reach maximum abundance from 9 to 18 m between Cape Fear, NC and Cape Canaveral, FL. In the study area, *O. stephensoni* was most numerous in strata off South Carolina and North Carolina where 43 individuals/tow were collected. Catches decreased off Georgia to 29 individuals/tow and were lowest in strata off Florida (<1 individual/tow). Stratified mean catch per tow was highest in spring (120 individuals/tow) and declined markedly during other seasons (Table 5, Fig. 4).

Analysis of size composition indicated mean carapace width differed between strata and season. Largest crabs were found off Florida ($\bar{x}$ CW = 45 mm, n = 63), while average sizes off Georgia (n = 713) and South Carolina/North Carolina (n = 2,349) were 30 mm and 34 mm, respectively. *Ovalipes stephensoni* collected in fall were larger ($\bar{x}$ CW = 42 mm, n = 273) than those collected during other seasons (winter: $\bar{x}$ CW = 38 mm, n = 199; spring: $\bar{x}$ CW = 30 mm, n = 1,591; summer: $\bar{x}$ CW = 36 mm, n = 1,062).

Analysis of sex ratios by season indicated signif-

icantly more female than male *O. stephensoni* were collected (Table 6). Male crabs ($\bar{x}$ CW = 34 mm, n = 1,278) were comparable in size to females ($\bar{x}$ CW = 33 mm, n = 1,840); however, most of the crabs collected were immature, being smaller than sizes (short carapace width) at full sexual maturity of 61 mm for males and 51 mm for females given by Haefner (1985). This supports previous observations (Williams 1984) that there is a positive size-depth relationship for the species.

Callinectes similis

The lesser blue crab occurs in the oceanic littoral zone where it is commonly associated with the blue crab. Along the east coast of the United States, *C. similis* ranges from Delaware Bay to Key West, but is primarily a Carolinean species. Northern occurrence of the species occurs seasonally during years with favorable annual temperature (Williams 1984).

Callinectes similis ranked fourth in terms of number of individuals among all species collected in this study and occurred in 64% of the trawl tows made. The species constituted 10% of the total biomass, which was considerably less than *C. sapidus* (Table 1). The stratified mean catch per tow for numbers and weight was highest in summer and fall (Table 5). Tagatz (1967), who did not distinguish between

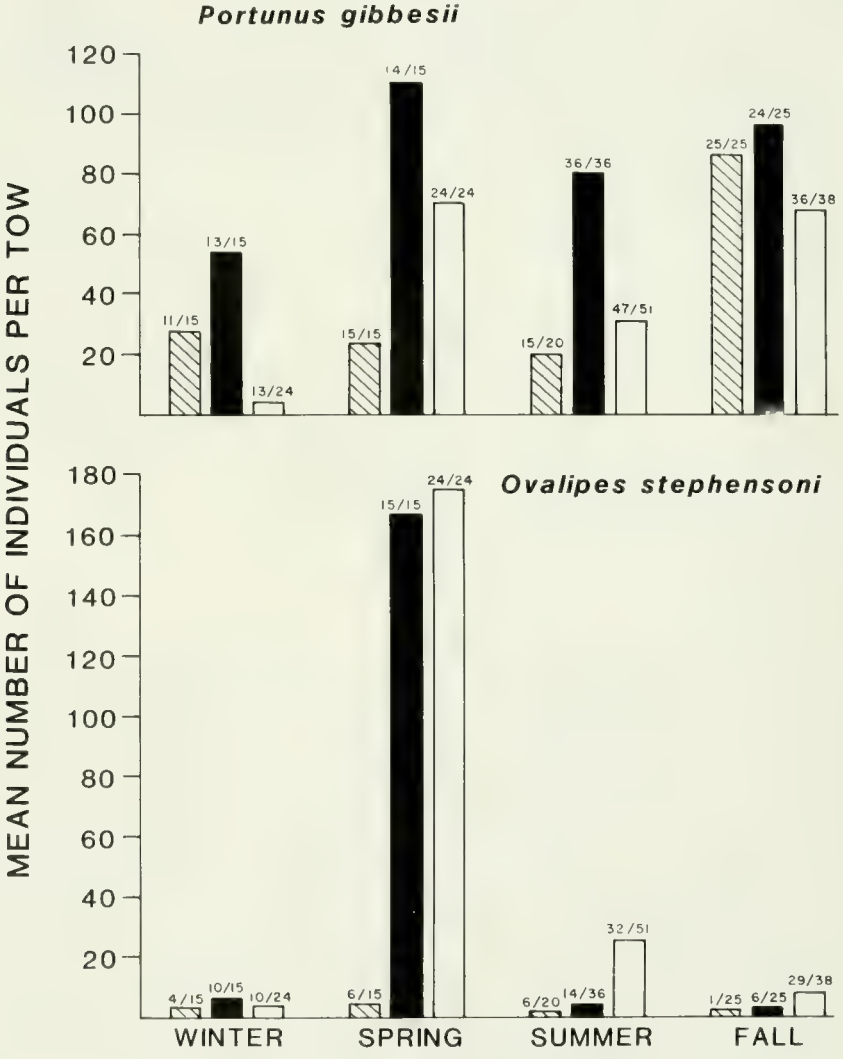


FIGURE 4.—Seasonal catch rates of the dominant decapod and stomatopod species.

TABLE 5.—Stratified mean catch per tow of 15 most numerous species caught during the coastal study.

Species	Stratified mean catch per tow							
	Winter		Spring		Summer		Fall	
	No.	Weight	No.	Weight	No.	Weight	No.	Weight
Portunus gibbesii	26	0.240	54	0.473	41	0.156	79	0.588
Squilla empusa	28	0.335	40	0.580	42	0.635	31	0.515
Ovalipes stephensoni	4	0.096	120	0.578	14	0.151	4	0.075
Callinectes similis	<1	0.016	4	0.091	34	0.836	35	0.571
Penaeus setiferus	15	0.289	2	0.063	12	0.260	30	0.791
Penaeus aztecus	<1	—	<1	0.005	44	0.722	2	0.048
Portunus spinimanus	3	0.096	13	0.214	14	0.207	11	0.269
Ovalipes ocellatus	1	0.063	17	0.344	12	0.389	4	0.164
Hepatus epheliticus	<1	0.007	5	0.138	12	0.357	10	0.352
Squilla neglecta	<1	0.002	9	0.120	7	0.065	4	0.059
Callinectes sapidus	2	0.361	6	1.316	8	1.202	1	0.214
Arenaeus cribrarius	<1	0.010	2	0.076	9	0.348	5	0.210
Trachypenaeus constrictus	5	0.014	2	0.005	1	0.001	6	0.019
Libinia emarginata	6	0.390	6	0.203	2	0.085	2	0.145
Penaeus duorarum	<1	0.005	9	0.152	2	0.020	3	0.031

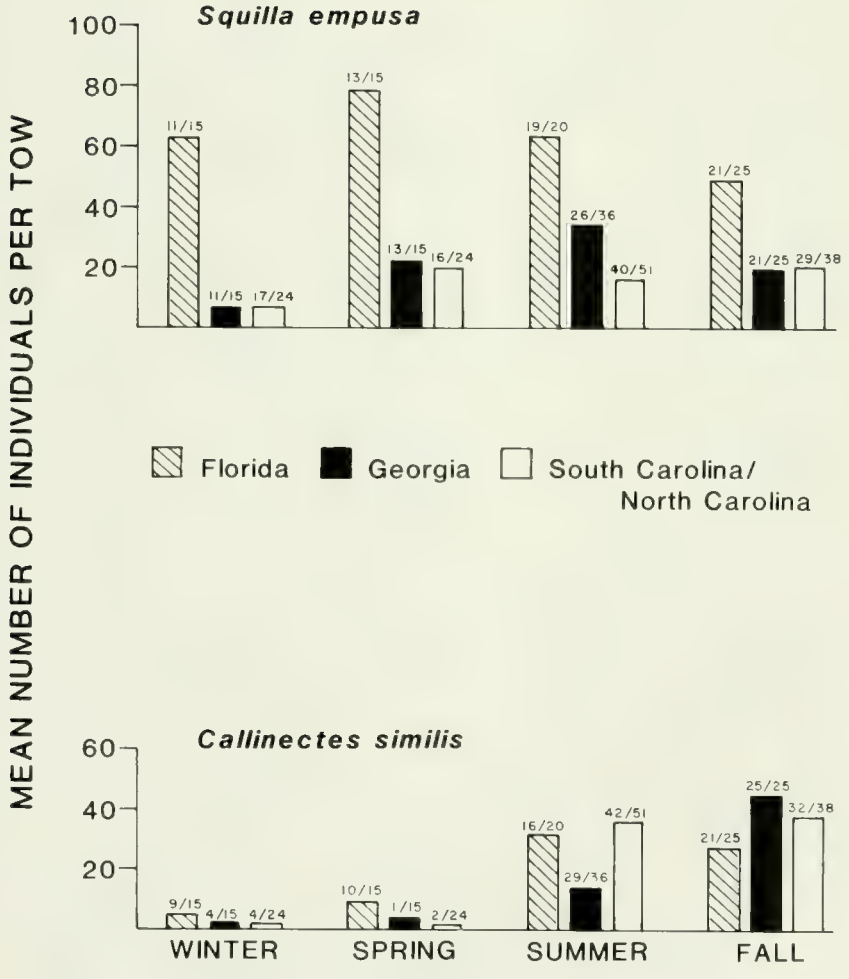


FIGURE 4.—*Continued.*

C. similis and *C. ornatus*, noted increased abundance from May to November with the largest catches in May, June, and October. Comparison of mean catch per tow between areas showed that *C. similis* was most abundant in strata off Florida and North Carolina/South Carolina during summer and in strata off Georgia during fall (Fig. 4). For all seasons, however, the mean catch per tow was highest for strata off North Carolina/South Carolina where an average of 24 individuals and 0.49 kg were taken per tow.

Size composition of *C. similis* differed between seasons with average size smallest in fall ($\bar{x}$ CW = 61 mm, n = 1,685). Average sizes during other seasons were spring (68 mm CW, n = 167); summer (67 mm CW, n = 2,558); and winter (64 mm CW, n = 36). The average size of individuals collected from strata off Florida ($\bar{x}$ CW = 72 mm, n = 1,025) was larger than those from Georgia ($\bar{x}$ CW = 59 mm, n = 1,111) and South Carolina/North Carolina ($\bar{x}$ CW = 65 mm, n = 2,310).

Sex ratios of *C. similis* indicated a significant

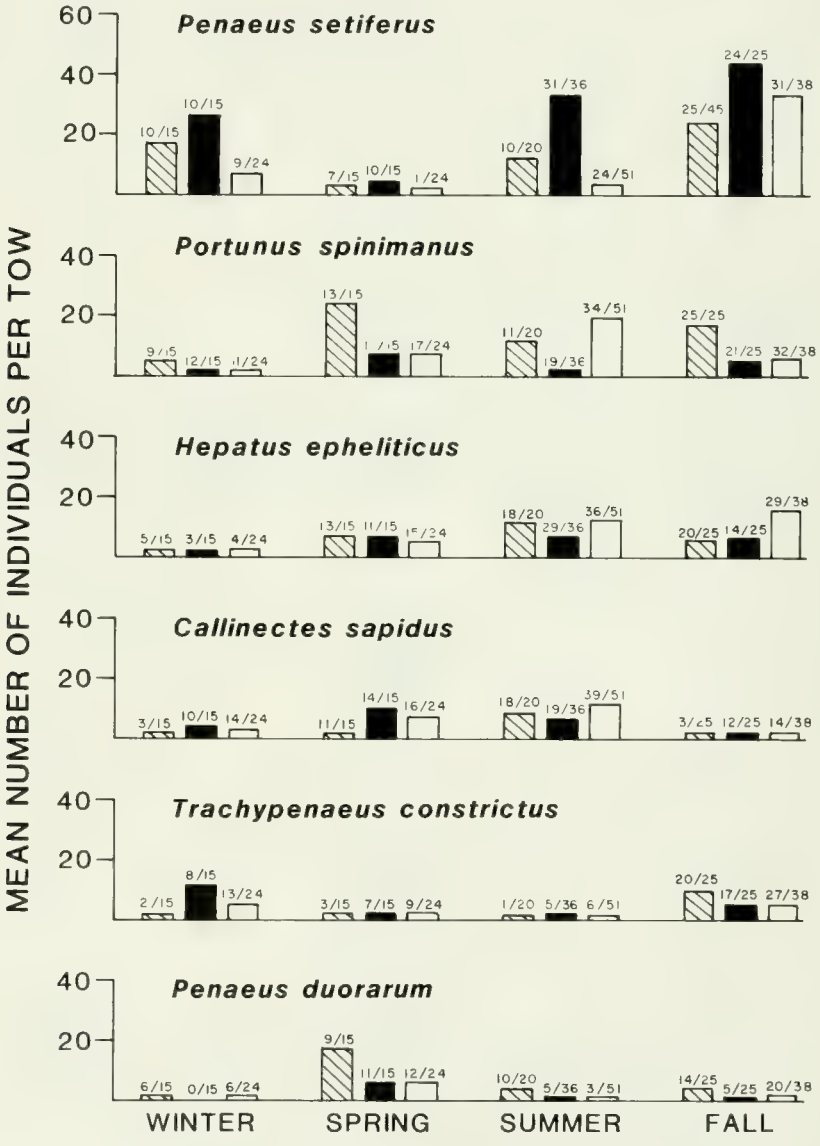


FIGURE 4.—*Continued.*

deviation from 1:1 during summer only (Table 6). Male *C. similis* were found to have a greater average size ($\bar{x}$ CW = 69 mm, n = 2,130) than females ($\bar{x}$ CW = 61 mm, n = 2,294). Of the 2,128 female *C. similis* examined for sexual maturity, 466 individuals were mature. Mature females ranged in size from 41 to 114 mm CW, while immature females were from 25 to 92 mm CW.

Penaeus setiferus

The white shrimp ranges from Fire Island, NY to Saint Lucie Inlet, FL and in the Gulf of Mexico from the Ochlocknee River, FL to Campeche, Mexico (Williams 1984). Along the Atlantic coast of the United States, white shrimp are most abundant in South Carolina, Georgia, and northeast Florida where the species constitutes a substantial commercial fishery (South Atlantic Fishery Management Council 1981). Within the region, white shrimp are concentrated in waters <16.5 m (Anderson 1956), but abundance of *Penaeus* spp. appears to be related to distance from shore with shrimp most abundant within five miles of the coast line

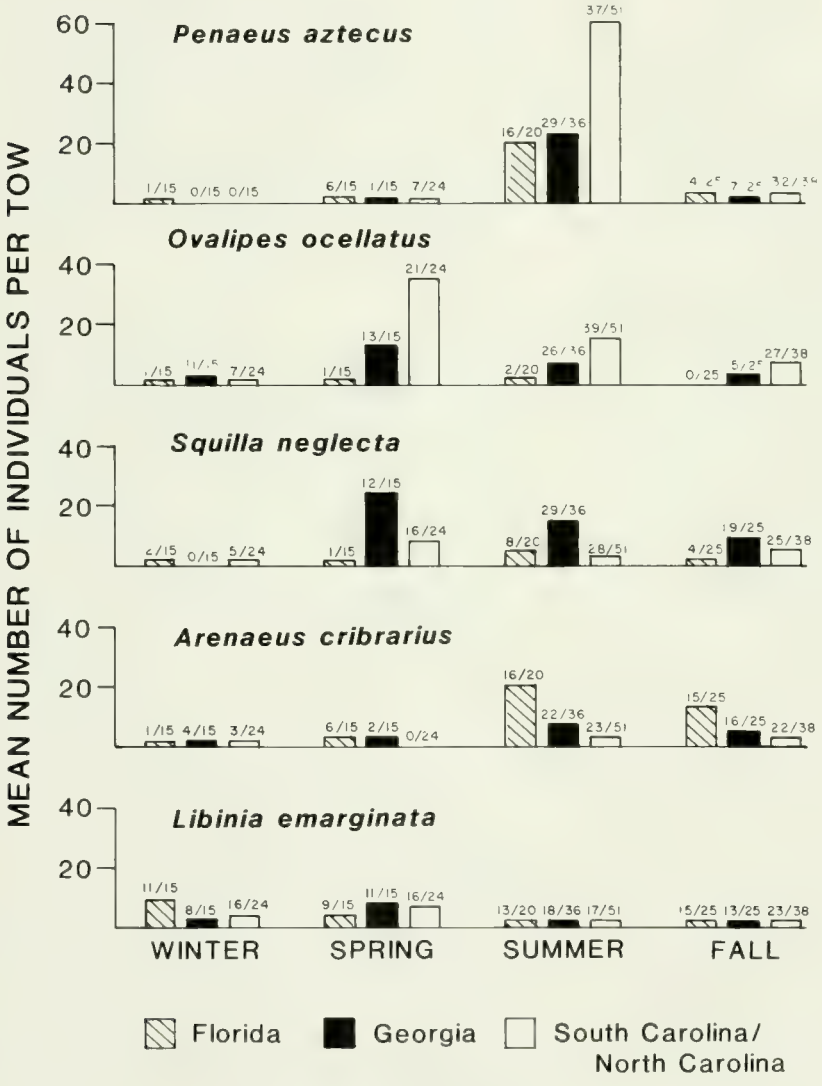


FIGURE 4.—*Continued.*

TABLE 6.—Frequency of males and females for species by season. * reflects significant deviation of M:F from 1:1 ($P < 0.05$) as determined by χ^2 analysis.

Species	Winter	Spring	Summer	Fall
Portunus gibbesii	*	*	*	*
Male	239	563	890	1,144
Female	369	739	1,019	1,908
Total	608	1,302	1,909	3,052
Ovalipes stephensoni	*	*	*	*
Male	84	694	398	102
Female	114	895	661	171
Total	198	1,589	1,059	273
Callinectes similis			*	
Male	18	77	1,166	874
Female	18	90	1,378	814
Total	36	167	2,544	1,688
Portunus spinimanus		*		
Male	74	254	450	395
Female	69	335	443	383
Total	143	589	893	778
Ovalipes ocellatus				*
Male	28	289	457	149
Female	30	269	502	208
Total	58	558	959	357
Hepatus epheliticus		*	*	*
Male	14	100	320	231
Female	16	206	718	541
Total	30	306	1,038	772
Callinectes sapidus	*	*	*	*
Male	7	8	23	12
Female	145	306	863	116
Ovigerous	0	214	405	2
Total	152	314	886	128
Arenaeus cribrarius		*	*	*
Male	9	61	446	205
Female	4	36	348	157
Total	13	97	794	362
Libinia emarginata	*			
Male	161	158	92	107
Female	120	153	86	89
Total	281	311	178	196

(South Atlantic Fishery Management Council 1981).

Penaeus setiferus was the most abundant penaeid collected in this survey, and it constituted 9% of the total catch of decapod crustaceans (Table 1). This species accounted for 10% of the total biomass of stomatopods and decapods and occurred in 63% of the 303 collections made. The stratified mean catch per tow differed among seasons, with abundance greatest in fall (30 individuals/tow) and lowest in spring (2 individuals/tow) (Table 5). This seasonal difference in abundance of *P. setiferus* in the nearshore coastal zone is explained by movement of white shrimp from estuaries to offshore waters in fall. This emigration is associated with declining water temperatures (Lindner and Anderson 1956; Pullen and Trent 1970). White shrimp enter the estuaries as postlarvae in May, grow rapidly in the estuarine nursery grounds, and move seaward through late summer and fall (Weymouth et al. 1933).

Within the three areas sampled, white shrimp were most abundant in strata off Georgia during every season except spring (Fig. 4). This may result from a predominantly southward movement of white shrimp during fall, winter, and summer as discussed by Shipman (1980).

The mean total length of white shrimp differed by season with largest individuals occurring in spring ($\bar{x}$ = 162 mm, n = 93). The larger average size at this time was probably influenced by occurrence of female roe shrimp that move to nearshore coastal waters from estuaries during the spring (Lindner and Anderson 1956; Joyce and Eldred 1966; Harris 1974; Music 1979; Farmer et al. 1978). The mean size of shrimp collected was largest in strata off North Carolina/South Carolina ($\bar{x}$ = 152 mm, n = 1,439), while those from strata off Georgia and Florida averaged 145 mm (n = 2,269) and 142 mm (n = 1,121), respectively.

Penaeus aztecus

Brown shrimp occur from Martha's Vineyard, MA to the Florida Keys and into the Gulf of Mexico where they occur on the Sanibel grounds, in Appalachicola Bay, and to northwestern Yucatan (Williams 1984). Along the Atlantic coast of the United States, *P. aztecus* is most abundant off North and South Carolina (Cook and Lindner 1970).

Brown shrimp were collected in 51% of the trawl tows made during the study and were the second most abundant *Penaeus* collected (Table 1). The stratified mean catch per tow was much greater in summer (44 individuals/tow) than during the other seasons when <2 individuals/tow were collected (Table 5). Brown shrimp usually occupy the estuarine nursery grounds from March through July before emigrating to coastal waters in August. Emigration, however, may be delayed if cooler than normal temperatures occur in spring (South Atlantic Fishery Management Council 1981). The summer cruise occurred from mid-July into September, which overlapped the period when brown shrimp emigrated from the estuary. During the summer sampling period, brown shrimp abundance was greatest in strata sampled off North Carolina/South Carolina (Fig. 4). Abundance during other seasons was too low to assess any difference between areas.

The mean total length of brown shrimp was greatest in summer ($\bar{x}$ = 126 mm, n = 2,718) and fall ($\bar{x}$ = 126 mm, n = 214) following emigration from the estuaries. Size at emigration for brown shrimp has been reported to be 100–105 mm (Joyce 1965) and 60–103 mm (Trent 1967). Off North Carolina, *P. aztecus* enters the commercial fishery in June at a size of 100 mm (South Atlantic Fishery Management Council 1981). Mean size of brown shrimp was largest off Georgia ($\bar{x}$ = 138 mm, n = 871) and Florida ($\bar{x}$ = 127 mm, n = 493), while those from strata off North Carolina and South Carolina averaged 119 mm (n = 1,600). The capture of larger shrimp further south may result from migration of individuals to waters off Georgia and Florida. These shrimp are probably supplied by the sounds and estuaries of North and South Carolina. Tagging studies off North Carolina indicate that brown shrimp move to the south and to deeper, nontrawlable waters once they leave the sounds (Purvis and McCoy 1974). Shipman (1980) noted few recaptures of brown shrimp tagged off Georgia and suggested that lower return rates may indicate offshore movement of brown shrimp, out of the nearshore trawling grounds.

Portunus spinimanus

This common portunid of the inner continental shelf ranges from New Jersey to southern Florida (Powers 1977), often co-occurring with *P. gibbesii*. Camp et al. (1977) found *P. spinimanus* to be one of the commonest decapod crustaceans in samples from nearshore east Florida waters with salinity of 32–39‰ and temperature ranging from 19.2° to 32°C.

In the present study, *P. spinimanus* was the 7th most numerous species (4.1% of the total catch) and the 11th most important by weight (4%) (Table 1). This species occurred at 73% of the trawl stations from all seasons. The stratified mean catch per tow was lowest in winter (3 individuals/tow). Catch per tow values by stratum were higher in spring (13 individuals/tow) and summer (14 individuals/tow), but decreased to 11 individuals/tow in fall (Table 5). Catch of *P. spinimanus* per tow differed among areas with most individuals collected in trawl tows off Florida (15 individuals/tow). Increased abundance in strata off Florida was observed for every season except summer (Fig. 4).

The size composition of *P. spinimanus* in trawl catches differed between strata and seasons. Mean carapace width was largest for individuals collected off Florida ($\bar{x}$ CW = 54 mm, n = 974) and Georgia ($\bar{x}$ CW = 53 mm, n = 343), while those collected in combined strata off South Carolina and North Carolina averaged 46 mm CW (n = 1,129). Largest individuals were collected in winter ($\bar{x}$ CW = 58 mm, n = 144) and fall ($\bar{x}$ CW = 56 mm, n = 782). The smaller average size of individuals collected in spring ($\bar{x}$ CW = 48 mm, n = 601) and summer $\bar{x}$ CW = 46 mm, n = 919) may reflect an influx of small crabs from the previous fall hatch.

Analysis of sex ratio by season indicated no significant deviation from unity except during spring when female *P. spinimanus* outnumbered males (Table 6). Average size was similar for males ($\bar{x}$ CW = 51.4 mm, n = 1,172) and females ($\bar{x}$ CW = 49.8 mm, n = 1,230).

Ovalipes ocellatus

This portunid crab has a broad geographic range from Canada to Georgia (Williams 1984). Abundance decreases in southern latitudes, apparently in response to lessened tolerance to warm-water temperatures (Vernberg and Vernberg 1970). In the present study, *O. ocellatus* occurred more frequently than *O. stephensoni*, but was not as numerous (Table 1). Abundance of this crab decreased from the northern to southern area, with most individuals collected in trawl catches off North Carolina/South Carolina (14 individuals/tow) (Fig. 4). Abundance in strata off Georgia was 6 individuals/tow, while <1 individual/tow was caught off Florida. The stratified mean catch per tow differed among season with most individuals collected in spring (Table 5).

Average size of *O. ocellatus* differed among areas. The average size of individuals collected in strata off Florida was larger ($\bar{x}$ CW = 65 mm, n = 11) than that from other areas (Georgia: $\bar{x}$ CW = 53 mm, n = 588; South Carolina/North Carolina: $\bar{x}$ CW = 51 mm, n = 1,340). Seasonal differences in size composition were noted as well, with average carapace width smallest in spring ($\bar{x}$ CW = 48 mm, n = 558). This may reflect occurrence of juveniles from a fall-winter hatch (Dudley and Judy 1971). Average size of individuals during other seasons was winter ($\bar{x}$ CW = 59 mm, n = 58), summer ($\bar{x}$ CW = 52 mm, n = 966), and fall ($\bar{x}$ CW = 57 mm, n = 357).

No significant seasonal difference in sex ratio was noted, with the exception of fall when females were more numerous than males (Table 6). Male *O. ocellatus* ($\bar{x}$ CW = 54 mm, n = 923) were larger than females ($\bar{x}$ CW = 50 mm, n = 1,009).

Hepatus epheliticus

The known range for this crab extends from Chesapeake Bay to southern Florida where it is a common inhabitant of nearshore waters. Evidence suggests it buries in sandy substrate (Williams 1984) and may be nocturnally active (Powers 1977).

Hepatus epheliticus occurred throughout the study area and was present in 65% of the collections made during all seasons (Table 1). Abundance differed among seasons with the stratified mean catch per tow being highest in fall (10 individuals/tow) and summer (12 individuals/tow) (Table 5). Number of individuals per tow also differed between areas with highest catches noted from strata off South Carolina and North Carolina (10 individuals/tow) (Fig. 4). Larger crabs were noted in this region with a mean carapace width ($\bar{x}$ CW) of 58 mm (n = 1,176). The mean size of *H. epheliticus* from Georgia coastal waters was 58 mm (n = 526), while those from strata off Florida averaged 54 mm (n = 456). There was a noticeable decrease in size and number of crabs collected in winter ($\bar{x}$ CW = 38 mm, n = 30) compared with sizes noted for other seasons (spring: $\bar{x}$ CW = 52 mm, n = 306; summer: $\bar{x}$ CW = 57 mm, n = 1,050; fall: $\bar{x}$ CW = 60 mm, n = 772). This may reflect movement of larger crabs further offshore during the winter.

Female *H. epheliticus* significantly outnumbered male crabs during every season except winter (Table 6). Carapace width was similar among the sexes (male $\bar{x}$ CW = 58 mm, n = 663) (female $\bar{x}$ CW = = 57 mm, n = 1,479).

Squilla neglecta

This stomatopod species has a more disjunct distribution than its congener, *S. empusa*, and occurs from North Carolina to Florida, the Gulf of Mexico from western Florida to Texas, and southwest to Brazil (Gore and Becker 1976). *Squilla neglecta* was found by Camp (1973) to co-occur with *S. empusa* on the central west Florida Shelf where both were most abundant at 18 m depths.

Squilla neglecta occurred in 49% of the trawl tows and was most abundant in spring (9 individuals/tow) (Table 5). The number of individuals per tow was highest in strata off Georgia during every season except winter when none occurred there (Fig. 4).

Callinectes sapidus

The blue crab occurs along the western Atlantic coastline from Maine to northern Argentina, with the main commercial fishery in Chesapeake Bay (Williams 1984). Blue crabs occur on a variety of bottom types and are mainly abundant out to depths of 35 m.

Callinectes sapidus ranked first in terms of biomass, making up about 19% of the entire catch of decapods and stomatopods (Table 1). Blue crabs occurred in 173 of the 303 trawl tows made during the survey.

The stratified mean catch per tow for number and weight was greatest in the coastal zone during spring and summer (Table 5). Comparison of catches between areas showed abundance was comparable for strata off Georgia and North Carolina/South Carolina during all seasons (Fig. 4).

Size composition of blue crabs differed between seasons with the average carapace width being greatest in winter and spring (Fig. 5). Mean carapace width was similar between areas, however, with those collected off Florida averaging 137 mm (n = 164) and those from strata off Georgia (n = 485) and North Carolina/South Carolina (n = 835) averaging 139 mm and 138 mm, respectively.

Sex ratios were overwhelmingly dominant in terms of female *C. sapidus* for each season (Table 6). No ovigerous female crabs were collected in winter and only two individuals were found in fall collections. During spring and summer, however, the number of ovigerous females constituted 70% and 47% of the catch of female crabs, respectively. Among non-ovigerous females (n = 809), 95% of the blue crabs were mature.

Greater numbers of females in the coastal zone are expected in view of the life history of the blue crab. With the exception of the breeding season, when females migrate into lower salinity waters of the estuary, they are usually found near the mouths of estuaries where the eggs are spawned and hatch. Most spawning occurs in spring and early summer, with the season becoming progressively shorter from Florida to North Carolina (Norse 1977). Males, however, remain in the middle to upper reaches of estuaries as juveniles and adults (Gunter 1950; Hildebrand 1954).

Arenaeus cribrarius

This portunid is a common inhabitant of the shallow coastal zone along beaches (Hoese 1972; Williams 1984). The known geographic range extends from Massachusetts to Brazil. It occurs abundantly in the penaeid shrimp grounds of the Gulf of Mex-

ico (Hildebrand 1954). Anderson et al. (1977) seined 422 specimens in the surf at Folly Beach, SC and *A. cribrarius* was the most abundant macroinvertebrate collected in the same area by DeLancey (1984). In the present study, *A. cribrarius* constituted only 2% of the total catch of decapods and stomatopods but occurred in 43% of the total collections (Table 1). Mean catch per tow increased from northern to southern sampling areas, with highest catches (10 individuals/tow) off Florida. Catches decreased to 5 individuals/tow off Georgia to 2 individuals/tow off North Carolina/South Carolina. The stratified mean catch per tow showed a seasonal trend with highest catch occurring in summer and fall (Table 5). This corresponds with observations reported by Anderson et al. (1977) who found a positive correlation of number of crabs with water temperature.

Average carapace width was greatest for individuals collected off South Carolina/North Carolina ($\bar{x}$ CW = 82 mm, n = 286). Those from strata off Georgia (n = 436) and Florida (n = 544) averaged 78 mm. Size differences were noted between seasons, as well; however, the small number of individuals collected in winter (n = 13) did not provide adequate information on size composition for that season. During spring ($\bar{x}$ CW = 81 mm, n = 97), summer ($\bar{x}$ CW = 77 mm, n = 794), and fall ($\bar{x}$ CW = 83 mm, n = 362), the size composition of the catch was similar.

The M:F ratio was significant for every season except winter (Table 6). Male *A. cribrarius* were larger ($\bar{x}$ CW = 82 mm, n = 721) than females ($\bar{x}$ CW = 76 mm, n = 545).

Trachypenaeus constrictus

This penaeid shrimp is caught incidentally in the commercial shrimp fishery along the southeastern and Gulf coasts. Eldred (1959) reported that *T. constrictus*, along with *T. similis*, constituted 7% of the annual catch in the Tortugas area of Florida. In the South Atlantic Bight, *T. constrictus* was most abundant in the 9–18 m depth zone sampled by Wenner and Read (1981, 1982).

This species was seasonally abundant in collections from the coastal zone, with stratified mean catch per tow highest in fall (6 individuals) and winter (5 individuals) (Table 5). Increased abundance of the species during fall and winter was previously noted by Wenner and Read (1981, 1982) and is probably due to recruitment from spawning in spring and late summer (Williams 1969; Anderson 1970; Subrahmanyam 1971). The number of individuals per tow did not noticeably differ between the areas sampled (Fig. 4).

Libinia emarginata

The common spider crab ranges from Nova Scotia to south Florida where it occurs mostly on mud and mud-sand bottom in shallow water (Powers 1977). This species was reported by Hildebrand (1954) to be the most common large spider crab on the western Gulf of Mexico shrimping grounds. Winget et al. (1974) found *L. emarginata* seasonally most abundant in spring and summer in Delaware Bay where it was common in mud of sloughs. This species ranked 14th in overall abundance in the current study and occurred in 56% of the trawl collections (Table 1). Abundance of *L. emarginata* was nearly equal between the three areas: 4 individuals/tow off Florida, 3 individuals/tow off Georgia, and 3 individuals/tow off North Carolina/South Carolina. The stratified mean catch per tow differed among seasons with abundance highest in winter and spring (Table 6).

Carapace length was similar between areas, with largest individuals collected off Georgia ($\bar{x}$ CL = 54 mm, n = 232), while those from Florida and North Carolina/South Carolina waters averaged 52 mm (n = 283) and 50 mm (n = 451), respectively. Analysis of size frequencies by season (not shown) indicated a broad range of sizes. Small individuals, reportedly associated with the coelenterate *Stomolophus meleagris* (Hildebrand 1954), occurred in low numbers during every season. Average size of the sampled individuals was lowest in spring ($\bar{x}$ CL = 47 mm, n = 312) and summer ($\bar{x}$ CL = 50 mm, n = 179), while those collected in fall ($\bar{x}$ CL = 57 mm, n = 193) and winter ($\bar{x}$ CL = 54 mm, n = 282) were slighter larger.

Sex ratios were significantly different from unity in winter, when males dominated (Table 6). Winget et al. (1974) also noted dominance by male *L. emarginata* in winter. Carapace length differed between the sexes, with males slightly larger ($\bar{x}$ CL = 53 mm, n = 514) than females ($\bar{x}$ CL = 50 mm, n = 447).

Penaeus duorarum

Pink shrimp occur from southern Chesapeake Bay to the Florida Keys, along the coast of the Gulf of Mexico to the southern Yucatan Peninsula (Williams 1984). In the southern United States, *P. duorarum* occurs in commercial quantities only off North Carolina. Pink shrimp reach maximum abun-

dance in the coastal zone at depths from 11 to 37 m (South Atlantic Fishery Management Council 1981).

Pink shrimp were the least abundant *Penaeus* collected in this study (Table 1). They were collected in 101 of the 303 trawl tows made. The stratified mean catch per tow was highest for collections in spring when 0.15 individuals per tow were collected (Table 5). During spring, catches were highest in strata off Florida (Fig. 4). The average size of pink shrimp was greatest in spring ($\bar{x}$ TL = 121 mm, n = 502). Mean sizes during other seasons were winter ($\bar{x}$ TL = 113 mm, n = 11), summer ($\bar{x}$ TL = 95 mm, n = 101), and fall ($\bar{x}$ TL = 106 mm, n = 209). Average total length decreased from northern to southern areas as follows: North Carolina/South Carolina ($\bar{x}$ = 119 mm, n = 256), Georgia ($\bar{x}$ = 114 mm, n = 108), Florida ($\bar{x}$ = 111 mm, n = 459).

The increased abundance and size of shrimp in spring probably relates to their movement to the nearshore zone then. In North Carolina, pink shrimp emigrate from the estuaries in May and June, at which time spawning takes place (Williams 1984). Kennedy and Barber (1981) reported that movement offshore of Cape Canaveral begins in April and May. The larger average size of pink shrimp in spring probably reflects the presence of roe-bearing females in the coastal zone at that time.

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STATUS OF THE TILEFISH, *LOPHOLATILUS CHAMAELEONTICEPS*, FISHERY OFF SOUTH CAROLINA AND GEORGIA AND RECOMMENDATIONS FOR MANAGEMENT

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ABSTRACT

We used a sex- and age-structured model and CPUE data from commercial and research vessels to assess the current status of the tilefish, *Lopholatilus chamaeleonticeps*, substock off South Carolina and Georgia. Based on commercial CPUE data and assumed natural mortality (M) rates of 0.10–0.25, we estimated that adult population density prior to fishing ranged from 603 to 950 per km^2 and stock biomass ranged from 1,130 to 1,570 tonnes (t). Our estimates of the recommended fishing mortality rate ranged from 0.10 (M = 0.10) to 0.48 (M = 0.25), resulting in sustainable yields of 40 (M = 0.10) to 82 t (M = 0.25) per year. We obtained higher estimates of virgin population density (883–1,710 per km^2) when research CPUE data were used. Sustained yield estimates also were higher, ranging from 55 (M = 0.10) to 148 t (M = 0.25) per year. Average estimates of recommended yield from commercial and research CPUE data were 58 and 95 t, respectively. Observed yields in the developing fishery exceeded 100 t in 1981–84 and in 1986; however, current observations indicate that fishing effort has declined to a low level in response to reduced catches. Based on the assumption that commercial CPUE data better reflect population trends, we recommend that the annual harvest not exceed about 50 t, which should result in a stock biomass of about 400–800 t. Apparent limitations on sustainable yield from the fishery probably can be attributed to the long lifespan, slow growth rate, and sedentary nature of tilefish.

The tilefish, *Lopholatilus chamaeleonticeps*, is a large demersal species found along the outer continental shelf of North America from Nova Scotia to Key West, FL, along the Gulf coast to Campeche Bank, and off South America from Venezuela to Surinam (Freeman and Turner 1977). Tilefish are long-lived and have relatively slow growth rates (Harris and Grossman 1985). They are most common at depths of 100–400 m and water temperatures of about 9°–14°C (Freeman and Turner 1977). Abundance is greatest in areas where substrates are suitable for burrow construction (Able et al. 1982; Grossman et al. 1985) or afford other shelter such as scour depressions around boulders (Valentine et al. 1980) or rubble piles (Low and Ulrich 1983).

Katz et al. (1983) described two genetically distinct tilefish stocks through use of morphometric and electrophoretic data: one composed of tilefish from the Middle Atlantic Bight (MAB), and one composed of tilefish from the South Atlantic Bight (SAB) and Gulf of Mexico. Larval transport from the Gulf of Mexico to the SAB may be responsible for similarities in electrophoretic results for these two areas (Katz et al. 1983). Katz et al. (1983) suggested, however, that it may be necessary to manage these substocks separately because of their wide geographic separation. If true, this should be done with the understanding that Gulf of Mexico populations may serve as a source of recruits to SAB populations (Katz et al. 1983).

Tilefish have been harvested commercially in the MAB since 1915, with annual landings ranging from <1 tonne (t) to 4,500 t (Turner et al. 1983). Landings from the SAB and Gulf of Mexico were small prior to 1980 (Low et al. 1983). A limited number of tilefish were caught incidentally in the deepwater grouper fishery off South Carolina (Low and Ulrich 1982). Recreational catches were small because of the depth at which tilefish occur (Low and Ulrich 1982). Commercial fisheries have since developed in both the SAB and Gulf of Mexico, due in part to an interest in diversification within the shrimp industry (Low et al. 1983).

For the segment of the SAB tilefish fishery operating off South Carolina and Georgia, increased fishing effort has resulted in a substantial increase in tilefish landings since 1978 (Table 1). In addition, a considerable number of tilefish caught off Georgia

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TABLE 1.—South Carolina and Georgia tilefish, *Lopholatilus chamaeleonticeps*, landings from 1978 to 1986. Georgia landings of tilefish and blueline tilefish, *Caulolatilus microps*, were not reported separately routinely prior to 1985. Landings by gear type were available for 1980–85, however, so rod and reel and electric reel catches of unclassified tilefish (which are almost exclusively blueline tilefish) were excluded to yield a more accurate estimate of Georgia tilefish landings.

	Landings (metric tons)		
Year	South Carolina[1]	Georgia[2]	Total
1978	2.59	[3]0.10	2.69
1979	10.08	[3]0.02	10.10
1980	43.89	(confidential)	>43.89
1981	103.74	0.35	104.09
1982	163.78	7.99	171.77
1983	252.55	6.67	259.22
1984	190.44	39.49	229.93
1985	70.49	13.04	83.53
1986	142.96	(confidential)	>142.96

[1]Andy Jennings, Fisheries Statistics Office, South Carolina Wildlife and Marine Resources Department, Charleston SC, pers. commun. 1987.
[2]S. Gordon Rogers, Fisheries Statistics Coordinator, Georgia Department of Natural Resources, Brunswick, GA, pers. commun. August 1987.
[3]Georgia Department of Natural Resources. 1983. Georgia landings annual summary 1980. Ga. Dep. Nat. Resour., Coastal Resour. Div., Brunswick, GA.

from about 1982 to 1984 were landed in Florida; therefore, landings in Table 1 are a conservative estimate of removals from these grounds.

Low et al. (1983) provided a preliminary estimate of maximum sustained yield (MSY = 162 t) for the developing fishery. Their estimate was derived from Gulland's (1971) model MSY = $0.5MB_0$, where M was the natural mortality rate and B_0 was an estimate of virgin biomass. Our objective was to provide updated yield estimates for use in managing the tilefish fishery off South Carolina and Georgia. We base these estimates on the 9-yr sequence of catches from the developing fishery as well as recently obtained information on the growth, mortality, and reproductive biology of tilefish from this area.

METHODS

We used a deterministic sex- and age-structured model to simulate the developing tilefish fishery and to calculate sustainable yields. The model was based on the following assumptions and data sources. We assumed that the natural mortality rate (M) ranged from 0.10 to 0.25 (Harris and Grossman 1985). We used sex-specific estimates of weight-at-age because the von Bertalanffy growth curves and length-weight relationships used to calculate weight-at-age differed significantly by sex (Harris and Grossman 1985). We used maturity-at-length data (Erickson and Grossman 1986) to estimate maturity at age by using a logistic model:

$$p_{s,a} = 1/(1 + \exp(-b_{Mat}(L_{s,a} - L50_{Mat}))) \quad (1)$$

where $p_{s,a}$ was the proportion of sex-s, age-a fish that were sexually mature, b_{Mat} was a parameter affecting the steepness of the curve, $L_{s,a}$ was the standard length (SL) of sex-s fish at age a, and $L50_{Mat}$ was a parameter representing the length at which 50% of the fish were sexually mature. We assumed that the total biomass of sexually mature females (S_f) was an adequate measure of spawning potential.

We used a logistic model to relate selectivity to length:

$$sel_{s,a} = 1/(1 + \exp(-b_{Sel}(L_{s,a} - L50_{Sel}))) \quad (2)$$

where $sel_{s,a}$ was the proportion of sex-s, age-a fish that were vulnerable to fishing, b_{Sel} was a parameter affecting the steepness of the curve, and $L50_{Sel}$ was a parameter representing the length at which 50% of the fish were vulnerable to fishing. Based on length-frequency data (Harris and Grossman 1985), we assumed that female and male tilefish reached 50% vulnerability at about 475–500 and 500–525 mm SL, respectively. We used a slope parameter (b_{Sel}) of 0.05 so that selectivity-at-age in the simulated fishery ranged from about 0 at age 5 to 1.0 at age 11 (Harris and Grossman 1985). Parameter estimates used in the model are summarized in Table 2.

We assumed that the relationship between spawning stock size and subsequent recruitment was weak or nonexistent because 1) tilefish produce pelagic larvae (Fahay and Berrien 1981); 2) there may be substantial egg or larval transport between the Gulf of Mexico and SAB (Katz et al. 1983); and 3) tilefish are dependent on the availability of shelter (Valentine et al. 1980; Able et al. 1982; Low and Ulrich 1983; Grossman et al. 1985). To represent the stock-recruitment relationship, we used a Beverton-Holt curve of the following form (Kimura 1988):

$$N_{s,6}[t + 6] = \frac{0.5N_6[0]S_f[t]/S_f[0]}{1 - A(1 - S_f[t]/S_f[0])} \quad (3)$$

where $N_{s,6}[t + 6]$ was the number of sex-s, age-6 recruits in year $t + 6$, $N_6[0]$ was the virgin recruitment level for both sexes combined, and $S_f[t]$ and $S_f[0]$ were the biomass levels for spawning females in year t and prior to fishing, respectively. The pa-

rameter A controlled the degree of density-dependence. We assumed that recruitment was either constant (A = 1.000) or decreasing by 10% when the spawning stock was reduced by 50% (A = 0.889). Few studies have shown a statistically significant relationship between spawning stock and recruitment (Hennemuth 1979); nevertheless, recruitment would be expected to decline at high Fs. For that reason, we used the latter assumption to explore the effect of the stock-recruitment relationship on the form of the yield curve. Other investigators have used this approach to obtain conservative estimates of equilibrium yield when information on the stock-recruitment relationship was unavailable (Lenarz and Hightower 1985; Henry 1986; Hightower and Lenarz 1986).

We simulated the fishery using virgin recruitment levels of 10,000–200,000 6-yr-old fish. This range would result in virgin population sizes of 45,000–2.1 million fish, depending on the assumed level of natural mortality. Assuming that the area inhabitated by tilefish off South Carolina and Georgia is about 476 km^2 (Low et al. 1983), these population sizes correspond to adult densities of 95–4,400 per km^2. This appeared to be an adequate range of densities, given that estimates of tilefish burrow density in the Hudson and Veatch Canyons off southern New England ranged from 119 to 2,434 per km^2 in 1980 (Grimes et al. 1986). As Low et al. (1983) noted, the 1974–78 catch rates off southern New England (0.49–0.93 kg/hook; Grimes et al. 1980) were similar to the 1981–82 catch rate in the expanding fishery off South Carolina and Georgia (0.86 kg/hook).

TABLE 2.—Parameter estimates for the sex- and age-structured model of the tilefish fishery off South Carolina and Georgia.

	Female	Male
von Bertalanffy[1]		
L_∞	[2]792	922
k	0.090	0.086
t(zero)	−1.774	−0.920
Length-weight[1]		
b(1)	2.28572E-8	7.92693E-9
b(2)	2.974	3.141
Maturity-at-age		
b_{Mat}	0.030	0.018
$L50_{Mat}$	495	458
Selectivity-at-age		
b_{Sel}	0.05	0.05
$L50_{Sel}$	475, 500	500, 525

[1]Harris and Grossman (1985). Length-weight relationship: $w = b(1)L^{b(2)}$.

[2]The estimate of L_∞ in Harris and Grossman (1985) (895 mm) was incorrect.

Because tilefish catches were negligible prior to 1978, the starting (1978) number-at-age vector at each recruitment level was assumed to be the equilibrium vector obtained at an F of 0. We assumed that our estimates of total landings were much more reliable than our estimates of fishing effort. For that reason, we solved iteratively for the sequence of fishing mortality rates that would produce the observed 1978–86 catches (Methot in press). For example, we began by solving for the 1978 F that would produce the 1978 catch biomass, and then used that F to project the number-at-age vector remaining in 1979. [We assumed that the final (1986) F should not exceed 2.0 (an exploitation rate of 80–84%), in order to rule out those cases where the 1986 harvest was attained by removing essentially all remaining tilefish.] Using this approach to estimate F, the observed and simulated catch biomass levels match exactly, although the observed and simulated age distributions may be different. Note that if we had a similar degree of confidence in our estimates of catch and fishing effort, it might be more appropriate to minimize differences between observed levels and model estimates of both catch and effort (see for example, Deriso et al. 1983), rather than forcing the model to reproduce the catches exactly.

At each virgin recruitment level, we calculated the correlation between the estimated 1978–86 Fs and estimates of total effort based on CPUE data. We used two sources of CPUE data: 1) commercial snapper reel CPUE from 1980 to 1982 South Carolina vessels (Low and Ulrich 1983); and 2) mean longline CPUE from 1982 to 1985 research cruises aboard the RV *Georgia Bulldog*. Based on commercial snapper reel kg/landing (figure 13 in Low and Ulrich 1983), we estimated that observed annual landings would have required more than 22 trips in 1980, 89 in 1981, and 445 in 1982 (Table 3). Using research cruise estimates of longline kg/hook, we estimated that observed annual landings would have required 351,000 hooks fished in 1982, 1.9 million in 1983, 1.6 million in 1984, and 380,000 in 1985 (Table 3). The research catches were made using standard commercial longline gear (Harris and Grossman 1985). We also obtained a composite 1980–85 effort series using the ratio of hooks fished to trips in 1982 (Table 3), but our results were the same as when only research CPUE data were used.

At each level of natural mortality, we selected the virgin recruitment level that maximized the correlation between estimates of F and fishing effort. The selected recruitment level was used in the equilib-

TABLE 3.—Estimates of total effort based on commercial and research catch per unit effort (CPUE) and total commercial landings. Estimates of 1980–82 commercial CPUE (kg/landing) were based on landings by snapper reel vessels (figure 13, Low and Ulrich 1983). Research CPUE estimates (kg/hook) were based on longline sets aboard the RV *Georgia Bulldog*; each estimate is an average of seasonal averages from spring, summer, and fall cruises. Estimates of hooks fished in 1980 and 1981 were based on the commercial CPUE data, using the ratio of trips to hooks fished in 1982.

Year	CPUE		Total landings (kg)	Estimated trips	Estimated hooks fished
	Commercial (kg/landing)	Research (kg/hook)			
1980	1,950	—	>43,890	>22	(>17,331)
1981	1,174	—	104,090	89	(70,110)
1982	386	0.490	171,770	445	350,551
1983	—	0.137	259,220		1,892,117
1984	—	0.140	229,930		1,642,357
1985	—	0.220	83,530		379,682

rium yield calculations. Our approach for selecting virgin recruitment levels was based on the "tuning" process used in cohort analysis (Mohn 1983; Rivard 1983). In that approach, auxiliary information is used to "adjust" or "fine-tune" the estimates iteratively so that the output from cohort analysis "matches" some series of observations (Rivard 1983). The level of agreement between the observations and model predictions can be measured using correlation or regression techniques (Mohn 1983).

We obtained estimates of equilibrium yield by expressing the number of sex-s fish in each age class ($N_{s,a}$, $a = 6, \ldots, n$, where n refers to fish ages 30 and older) as a function of the number of age-6 female fish ($N_{f,6}$). Following Getz (1980), we assumed that

$$N_{s,a+1} = [\prod_{j=6}^{a} \exp(-Z_{s,j})]\, N_{f,6},$$

$$a = 6, \ldots, n-2 \tag{4}$$

$$N_{s,n} = [\prod_{j=6}^{n-1} \exp(-Z_{s,j})/(1 - \exp(-Z_{s,n}))]\, N_{f,6} \tag{5}$$

where $Z_{s,j}$ was the total mortality rate for sex-s, age-j fish. Using Equations (4) and (5), female spawning stock can be redefined as a function of $N_{f,6}$:

$$S_f = \sum_{a=6}^{n} N_{f,a}\, w_{f,a}\, p_{f,a} \tag{6}$$

$$= N_{f,6}[w_{f,6}\, p_{f,6} + \sum_{a=7}^{n-1} w_{f,a}\, p_{f,a} \prod_{j=6}^{a-1} \exp(-Z_{f,j})$$

$$+ w_{f,n}\, p_{f,n} \prod_{j=6}^{n-1} \exp(-Z_{f,j})/(1 - \exp(-Z_{f,n})] \tag{7}$$

$$= N_{f,6}\, \phi(F) \tag{8}$$

where $\phi(F)$ is the bracketed expression in Equation (7) for a specified F. We then substituted ($N_{f,6}\, \phi(F)$) for S_f and solved Equation (3) for the equilibrium recruitment level as a function of F:

$$N_{f,6} = (0.5\, N_6[0]\, \phi(F) - S_f[0] + \mathrm{A}S_f[0]/(\mathrm{A}\, \phi(F)). \tag{9}$$

The virgin spawning stock $S_f[0]$ was calculated from Equations (4) to (6) for the specified level of M and virgin recruitment. We used Equations (4)–(9) to calculate the equilibrium number-at-age vector and associated yield for Fs from 0.0 to 0.5.

Following Francis (1986), we defined the target fishing mortality rate as $F_{0.1}$ for the constant recruitment case and F_{msy} for the density-dependent case. $F_{0.1}$ was the fishing mortality rate at which the slope of the yield curve was one-tenth the slope of the curve at the origin (Gulland and Boerma 1973). Compared to managing for maximum sustained yield, the $F_{0.1}$ policy usually results in greater economic efficiency when constant recruitment is assumed (Gulland and Boerma 1973; Sissenwine 1981; Francis 1986). An additional advantage is that a larger spawning stock would be maintained (Sissenwine 1978). The less conservative F_{msy} policy was assumed to be appropriate for the more conservative density-dependent case. The recommended yields for the constant recruitment and density-dependent cases were the equilibrium yields at $F_{0.1}$ and F_{msy} respectively.

RESULTS AND DISCUSSION

Our approach for estimating virgin recruitment level was similar to stock reduction analysis (SRA) (Kimura et al. 1984; Kimura 1985) except that we used a more general model to represent stock dynamics. In both approaches, a model is fully specified and the sequence of Fs used to drive the model are those that would have produced the observed sequence of catches. A range of solutions can be obtained corresponding to a range of virgin recruitment levels, but the solution set can be restricted by comparing model predictions to auxiliary data.

We obtained similar 9-yr patterns of F at different levels of virgin recruitment, particularly at higher recruitment levels where Fs were low in all years (Fig. 1). For that reason, correlation coefficients were similar over a wide range of recruitment levels (Fig. 2). Stronger conclusions about the true level of virgin recruitment may be possible once additional years of catch and CPUE data become available.

Based on commercial snapper reel CPUE data, the virgin recruitment level that maximized the correlation between estimates of F and fishing effort ranged from 30,000 to 100,000, depending on the assumed selectivity parameters and level of natural mortality (Table 4, Fig. 2). Correlations were high at all virgin recruitment levels, with maximum values obtained at the lowest recruitment levels capable of sustaining the 1978–86 observed catches (in order to match the sharp decline in CPUE from 1980 to 1982). Estimates based on research cruise CPUE data were higher, ranging from 40,000 to 180,000 (Table 5, Fig. 2). In both cases, the results were much more sensitive to M than to the $L50_{Sel}$ parameter of the selectivity function (Tables 4, 5).

Based on these estimates of the virgin recruitment level, the adult population prior to fishing would have ranged from 287,000 to 452,000 fish (commercial CPUE) or 420,000 to 814,000 fish (research CPUE). Assuming 476 km^2 of tilefish habitat off South Carolina and Georgia (Low et al. 1983), the estimated density prior to fishing would have been 603–950 (commercial CPUE) or 883–1,710 (research CPUE) per km^2. We are not aware of other estimates of tilefish density prior to fishing. Submersible dives were made on the South Carolina tilefish grounds after the period of (assumed) heavy exploitation; unfortunately, no density estimates are currently available. Comparisons with the exploited MAB stock are of some interest because MAB catch rates in the late 1970s were similar to initial catch rates off South Carolina and Georgia (Low et al. 1983). Our density estimates were similar to the burrow density estimates from the MAB. Grimes et al. (1986) reported that burrow density in Hudson Canyon ranged from 1,815 per km^2 in 1980 to 1,132 in 1982. Estimates for Veatch Canyon ranged from 772 per km^2 in 1981 to 1,531 in 1984. Tilefish density in the MAB may be lower than these estimates because not all burrows may be occupied (Able et al. 1982). In addition, burrow density is highly variable (Able et al. 1987) and some burrows may be inhabited only during certain seasons, depending on water temperature (Grimes et al. 1986). Nevertheless, these comparisons suggest that the density estimates we generated from catch data were reasonable.

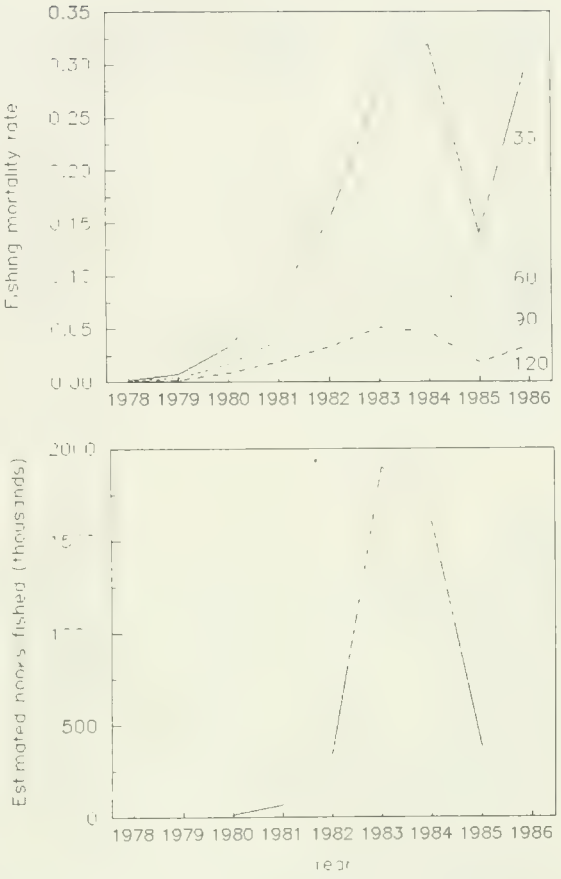

FIGURE 1.—Upper panel: estimated fishing mortality rates (F) from 1978 to 1986 at four (arbitrarily selected) levels of virgin recruitment (30,000–120,000 age-6 tilefish), assuming a natural mortality rate (M) of 0.10. Year-to-year changes in F were similar at other levels of M. Lower panel: estimates of fishing effort (hooks fished) based on commercial (1980–81) and research (1982–85) CPUE data.

TABLE 4.—Estimates of virgin levels of recruitment, adult population density, and biomass; recommended levels of fishing mortality, biomass, and yield; and 1987 biomass. Estimates were obtained from commercial CPUE data, using two sets of selectivity ($L50_{Sel}$) parameters, four levels of natural mortality (M), and two assumptions about the stock-recruitment relationship (A = 0.889 - recruitment dependent on spawning stock, A = 1.000 - recruitment constant).

	Female/male selectivity parameter $L50_{Sel}$							
	475/500 mm SL				500/525 mm SL			
M:	0.10	0.15	0.20	0.25	0.10	0.15	0.20	0.25
Virgin recruitment level (thousands)	30	40	70	90	30	40	70	100
Virgin population density (#/km^2)	662	603	811	855	662	603	811	950
Virgin biomass (t)	1,574	1,128	1,266	1,160	1,574	1,128	1,266	1,288
Recommended F (A = 0.889)	0.10	0.15	0.23	0.33	0.13	0.20	0.30	0.48
Recommended F (A = 1.000)	0.10	0.16	0.23	0.32	0.11	0.17	0.25	0.34
Recommended biomass (t) (A = 0.889)	553	437	511	485	509	408	504	535
Recommended biomass (t) (A = 1.000)	678	524	636	628	700	551	680	753
Recommended yield (t) (A = 0.889)	41	40	57	62	42	42	58	70
Recommended yield (t) (A = 1.000)	51	51	72	78	52	51	70	82
Estimated 1987 biomass (t)	624	247	468	435	636	261	484	584

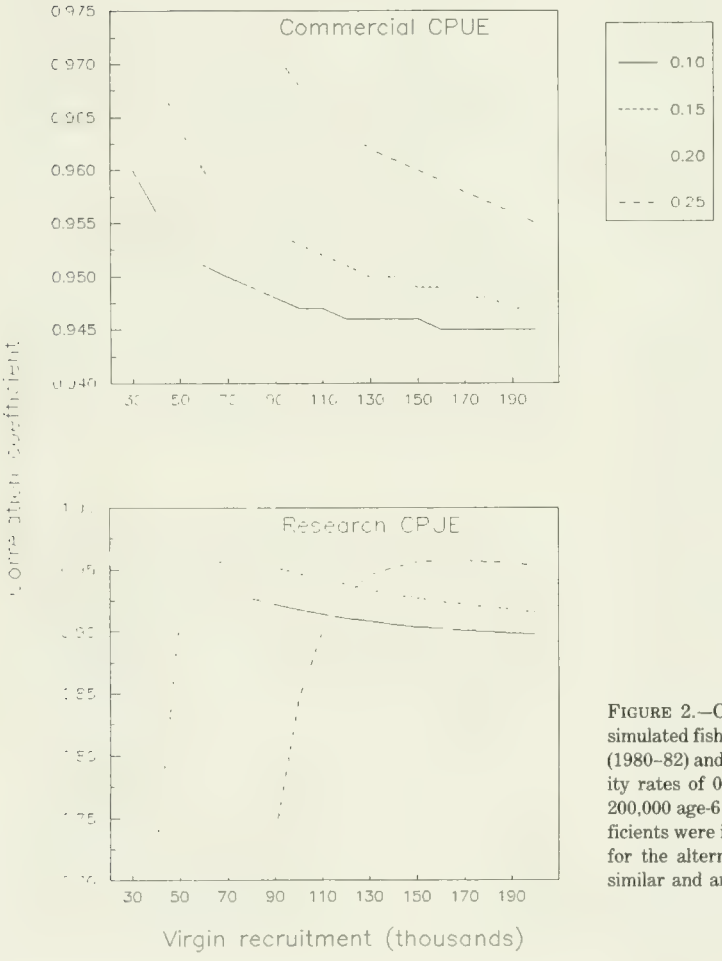

FIGURE 2.—Correlation between fishing mortality rates in the simulated fishery and estimates of fishing effort from commercial (1980–82) and research (1982–85) CPUE data, at natural mortality rates of 0.10–0.25 and virgin recruitment levels of 30,000–200,000 age-6 tilefish. Recruitment levels without correlation coefficients were inadequate to sustain the observed catches. Results for the alternative set of selectivity parameters ($L50_{Sel}$) were similar and are not shown here.

TABLE 5.—Estimates of virgin levels of recruitment, adult population density, and biomass; recommended levels of fishing mortality, biomass, and yield; and 1987 biomass. Estimates were obtained from research CPUE data, using two sets of selectivity ($L50_{Sel}$) parameters, four levels of natural mortality (M), and two assumptions about the stock-recruitment relationship (A = 0.889 - recruitment dependent on spawning stock, A = 1.000 - recruitment constant).

	Female/male selectivity parameter $L50_{Sel}$							
	475/500 mm SL				500/525 mm SL			
M:	0.10	0.15	0.20	0.25	0.10	0.15	0.20	0.25
Virgin recruitment level (thousands)	40	70	110	160	40	70	120	180
Virgin population density (#/km^2)	883	1,056	1,275	1,520	883	1,056	1,391	1,710
Virgin biomass (t)	2,098	1,974	1,989	2,062	2,098	1,974	2,170	2,319
Recommended F (A = 0.889)	0.10	0.15	0.23	0.33	0.13	0.20	0.30	0.47
Recommended F (A = 1.000)	0.10	0.16	0.23	0.32	0.11	0.17	0.25	0.34
Recommended biomass (t) (A = 0.889)	738	765	802	863	679	713	864	962
Recommended biomass (t) (A = 1.000)	904	917	999	1,117	932	965	1,165	1,355
Recommended yield (t) (A = 0.889)	55	71	89	109	56	73	100	126
Recommended yield (t) (A = 1.000)	69	90	114	139	70	89	120	148
Estimated 1987 biomass (t)	1,152	1,107	1,203	1,354	1,164	1,121	1,400	1,627

The two sets of CPUE estimates resulted in different conclusions about the current status of the stock. Based on commercial CPUE data, 1987 stock biomass was 22–45% of virgin biomass and 51–105% of the recommended level (Table 4). Estimated fishing mortality rates increased from about 0.1 in 1981 to a range of 0.3–1.4 in 1986 (Fig. 3). Based on research CPUE data, 1987 stock biomass was 55–70% of virgin biomass and 132–145% of the recommended level (Table 5). Estimated fishing mortality rates were much lower than from commercial CPUE data, increasing from about 0.08 in 1981 to 0.2 in 1986 (Fig. 3).

We believe that the results obtained from commercial CPUE data are far more likely, given recent reported declines in directed fishing. The decrease in landings observed in 1985 was attributed in part to reduced fishing pressure. A large group of boats from the Port Canaveral, FL area left the fishery, and a number of Georgia vessels began fishing further north (M. V. Rawson[3]). As of April 1988, most South Carolina longline vessels had switched to other fisheries and little directed tilefish fishing was occurring (R. Low[4]).

The difference in results for commercial and research CPUE estimates may be due to differences in areas fished. The RV *Georgia Bulldog* cruises were exploratory in nature, and catches were obtained primarily in the southern section of tilefish habitat off the Georgia coast (Harris and Grossman 1985). Early commercial effort was concentrated in the more northerly part of the tilefish habitat (Low et al. 1983). We recognize the commercial catch data provide a biased measure of abundance. Nevertheless, because South Carolina landings predominated in the developing fishery, we believe that commercial catch data from the primary fishing grounds will be a better overall measure of changes in abundance. For that reason, we restrict our remaining comments to results from the commercial CPUE data. Declines in commercial CPUE may underrepresent actual declines in abundance because fishermen presumably would change tactics over time in order to maintain high catch rates. If so, our use of commercial catch data may result in an optimistic estimate of current abundance.

We obtained equivalent estimates of 1987 biomass for the constant recruitment and density-dependent cases because of the short length of the data series, relative to the 6-yr lag between a reduction in spawning stock and subsequent lower recruitment to the fishery. Equilibrium yield curves differed substantially for the two recruitment assumptions (Fig. 4). Despite differences in equilibrium yield, recommended Fs were very similar for the two cases because of the different criteria used to develop F and yield recommendations (Table 4). Recommended yield was moderately higher under the optimistic constant recruitment assumption (Table 4). Recommended F was higher when $L50_{Sel}$ was increased; however, differences in recommended yield were negligible.

Estimated Fs differed substantially for the four levels of natural mortality (upper panel, Fig. 3). The large differences in 1984–86 Fs probably were due

[3]M. V. Rawson, University of Georgia Marine Extension Service, Brunswick, GA 31523, pers. commun. March 1987.

[4]R. Low, South Carolina Wildlife and Marine Resources Department, Charleston, SC 29412, pers. commun. April 1988.

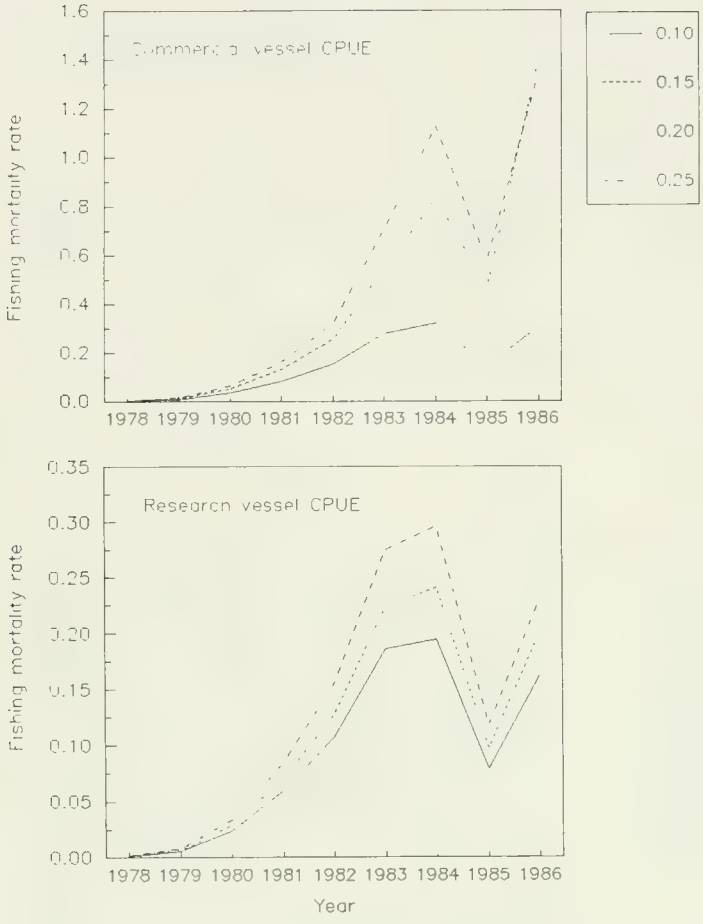

FIGURE 3.—Estimated fishing mortality rates (F) from 1978 to 1986 at natural mortality rates of 0.10–0.25. At each level of natural mortality, the virgin recruitment level was determined based on the correlation between F and estimated fishing effort, where estimates of effort were based on commercial vessel or research vessel CPUE. Results for the alternative set of selectivity parameters ($L50_{Sel}$) were similar and are not shown here.

to the lack of CPUE estimates for those years. Virgin biomass levels were similar at different levels of M, ranging from 1,130 t at M = 0.15 to 1,570 t at M = 0.10 (Table 4). Estimates of 1987 biomass were somewhat similar and relatively low, ranging from 247 t at M = 0.15 to 636 t at M = 0.10 (Table 4). Equilibrium yield curves differed in a predictable way at different levels of M (Fig. 4). Except at low Fs (<0.10), equilibrium yield increased as M increased, due to the higher estimates of virgin recruitment at higher levels of M. Recommended F was higher at higher levels of M, ranging from 0.10 at M = 0.10 to 0.48 at M = 0.25 (Table 4). Recommended yield increased from 41–52 t at M = 0.10 to 62–82 t at M = 0.25.

These results demonstrate that an important source of uncertainty in assessing tilefish stock status is the estimate of M. Harris and Grossman (1985) obtained 1982–83 catch curve estimates of Z equal to 0.25 for both female and male tilefish. Because the areas sampled by the RV *Georgia Bulldog* were thought to have received little fishing pressure, M could be as high as 0.25. Catch curve estimates of Z would be biased, however, if vulnerability to fishing increased with size. Turner et al. (1983) reported a decline in size at recruitment in the expanding MAB fishery and suggested that when larger tilefish were present, smaller ones either were less vulnerable to the gear or were avoided by fishermen. Z (and M) could be underestimated if vulnerability to fishing increased with size. Alternatively, Z (and M) could be overestimated if significant catches of predominantly older fish were made in the areas sampled by the RV *Georgia Bulldog*.

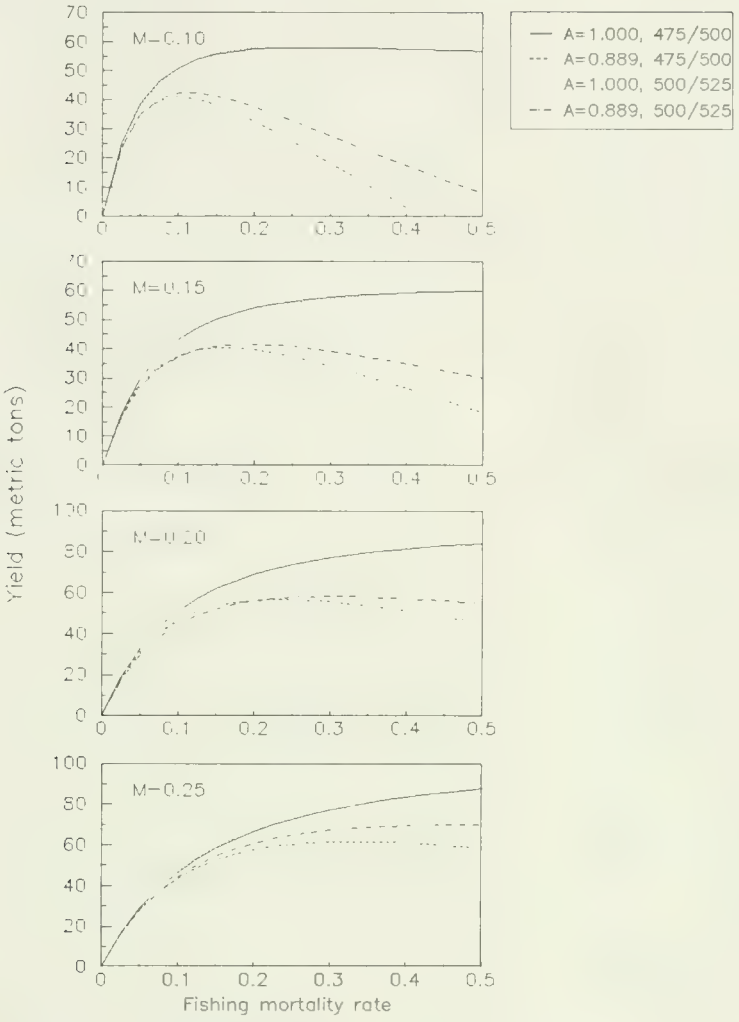

FIGURE 4.—Estimated equilibrium yield at four rates of natural mortality (M), two assumptions regarding the stock-recruitment relationship (A = 0.889 - recruitment dependent on spawning stock, A = 1.000 - recruitment constant), and two values for the female and male (F/M) selectivity parameter $L50_{Sel}$.

Evidence that M is less than 0.25 was provided by predictive models used to estimate M from the growth rate (k) and maximum age (Alverson and Carney 1975) or from k, L_∞, and mean water temperature (Pauly 1980). Estimates from the Alverson-Carney model were 0.107 (female) and 0.118 (male), whereas estimates from Pauly's method were 0.175 (females) and 0.163 (males) (Harris and Grossman 1985). Furthermore, Hoenig (1983) provided a model that predicts total mortality rate (Z) as a function of maximum age. Maximum observed age from May 1982 to August 1983 samples was 32 for female and 33 for male tilefish (Harris and Grossman 1985). Using Hoenig's model, Z would be 0.13 for each sex; therefore, that would be a maximum estimate of M.

A potential source of error in this assessment is the assumption that the selectivity pattern is constant over time. Recent observations (R. Low, fn. 4) indicate that the size at first vulnerability to fishing has decreased from about 1 kg (Harris and Grossman 1985) to about 0.45 kg. The decreasing size at recruitment increases the likelihood of recruitment overfishing because fish are being harvested well before the size at maturity (about 2–3 kg for females). Thus, the current model probably underestimates the impact of fishing. Higher F's could be sustained if small tilefish were not vulnerable to fishing; unfortunately, it is difficult to regulate age at entry for hook-and-line gear (Myhre 1974) and discard mortality under a minimum size regula-

tion would likely be substantial (Huntsman and Manooch 1978a).

A second potential source of error is the use of a deterministic model to represent recruitment. Changes in population size and CPUE are due not only to the impact of fishing but also to fluctuations in year-class strength. Because the estimates of virgin recruitment were based on changes in CPUE, fluctuations in recruitment that increase (decrease) the decline in CPUE would result in a lower (higher) estimate of virgin recruitment. Based on size-frequency data from the MAB tilefish fishery, Turner et al. (1983) suggested that fluctuations in tilefish year-class strength may be substantial. Using size- and age-frequency data collected off Georgia, Harris and Grossman (1985) found little evidence for strong fluctuations in year-class strength. Tilefish are somewhat difficult to age, however, so differences in year-class strength could be hidden by ageing errors.

A third source of error is the unknown number of fish caught off South Carolina or Georgia, but landed in Florida. The impact on the assessment would depend on the magnitude of the catches and the years in which the catches occurred. If we arbitrarily assume that actual annual removals were 25% higher than combined South Carolina-Georgia landings, recommended Fs would be unchanged, whereas estimates of virgin recruitment and recommended yield would increase by about 25%. Thus, if Florida removals could be accounted for, estimates of stock size would be more accurate, but the increase in recommended yield would be offset by the increased catches, and would not result in increased overall landings.

CONCLUSIONS

The results of this study provide estimates of the relationship between yield and fishing mortality and of the recommended level for F. Results obtained using commercial CPUE estimates indicate that sustainable harvests from the fishery are quite low, and would be obtained at Fs considerably lower than observed in the developing fishery. We obtained higher estimates of population size and sustained yield using research CPUE data; however, we believe that the commercial CPUE data better reflect population trends. We estimate that current stock size is about 200–600 t, compared with a recommended level of 400–800 t. If the stock could be rebuilt to the recommended level, it should support an annual harvest of about 50 t. A rebuilding strategy is feasible for tilefish because catches are low except when directed fishing occurs (G. Ulrich[5]). At present, however, there are no restrictions on the tilefish fishery and despite reductions in effort, catches are probably large enough to prevent the stock from rebuilding (G. Ulrich fn. 5).

Apparent limitations on sustainable yield of the tilefish fishery probably can be attributed to the demographic characteristics of the stock. In a typical fishery for a long-lived, slow-growing species, a few years of high catches are followed by a sharp decline and a subsequent period of low yield (Huntsman and Manooch 1978b; Leaman and Beamish 1984; Francis 1986). Long-lived, sedentary species, such as reef fishes, may be particularly vulnerable to overfishing, even though fishing intensity may be low or the method inefficient (Huntsman and Manooch 1978b). Because tilefish are long-lived, slow-growing, and sedentary (due to their dependence on the availability of shelter), a similar pattern of exploitation can be expected for the tilefish fishery off South Carolina and Georgia.

Leaman and Beamish (1984) recommended that conservative harvest strategies be developed for long-lived species until the evolutionary implications of longevity are better understood. They suggested that extreme longevity (>50 years) may be an adaptive response to ensure population persistence under reproductive uncertainty. For example, a long reproductive life might enable a species to inhabit deeper water (200–1,000 m) where few competitors or predators are found, even though recruitment into such areas may be highly variable (Leaman and Beamish 1984). If variability in recruitment has a significant effect on tilefish stocks, a conservative management strategy emphasizing maintenance of a range of age classes may be appropriate.

ACKNOWLEDGMENTS

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[5]G. Ulrich, South Carolina Wildlife and Marine Resources Department, Charleston, SC 29412, pers. commun. July 1987.

their observations on the current status of the fishery.

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HABITAT VALUE OF NATURAL VERSUS RECENTLY TRANSPLANTED EELGRASS, *ZOSTERA MARINA*, FOR THE BAY SCALLOP, *ARGOPECTEN IRRADIANS*

INGRID SMITH,[1] MARK S. FONSECA,[2] JOSE A. RIVERA,[3] AND KEITH A. RITTMASTER[4]

ABSTRACT

Bay scallops, *Argopecten irradians*, were used in a mark and recapture experiment to determine the habitat value of recently transplanted eelgrass, *Zostera marina*, meadows for fishery restoration and enhancement through stocking. The study site, adjacent to an island formed from dredge material, consisted of natural and transplanted eelgrass and of unplanted areas. Seventy-five marked bay scallops were placed in plots at a density of 2.2 scallops per m^2 on 20 February 1986. A month later, only 18 marked scallops were recovered; of these, 15 were found in the natural eelgrass beds. On the study site, 94% of 207 unmarked naturally occurring bay scallops were found in the natural eelgrass beds. Recovery of marked adult bay scallops was not affected by the distance from the dredge island; rather densities of natural scallop populations increased with distance from the island. A second, modified survey (30 March to 7 April 1986) was conducted specifically to examine the recovery of marked bay scallops; this survey again showed a high rate of loss both in the transplanted and unplanted areas.

The two surveys showed that recently transplanted eelgrass meadows do not provide the same habitat functions as natural meadows for bay scallops. Stocking of adult scallops in early stage eelgrass transplants to enhance or restore that fishery does not appear to be feasible. A protracted period of time may pass before habitat function is returned for the bay scallops in transplanted eelgrass meadows. Results from these surveys also illustrate the need for careful consideration in the placement of dredge material in the coastal environment.

Seagrass meadows form an essential habitat for a variety of marine organisms (Thayer et al. 1975, 1984; Kenworthy et al. 1988). These highly productive ecosystems provide refuge, food resources, and nursery grounds for a number of commercially and recreationally harvested species.

Recent concerns about loss of seagrass habitat in general (Thayer et al. 1984, 1985; Fonseca et al. 1985, 1987, 1988) have prompted research into ways in which that loss can be reduced. Since mitigation measures often require the creation of new seagrass meadows to replace damaged ones, it is critical that this trade-off provide a persistent habitat that is the functional equivalent of the one that is lost. Given our approach to creating seagrass beds by installing widely spaced planting units that coalesce in 1–2 years, it is possible that an artificially propagated bed will require a certain time interval before it will attain natural meadow functions. If these created beds do not provide similar functional values as natural ones or if they require a very long time to do so, then the entire concept of seagrass bed mitigation will have to be reexamined. These are critical questions, especially when seagrass restoration projects have not produced more acreage than was lost (Fonseca et al. 1988).

In the temperate zone, the dominant seagrass species is eelgrass, *Zostera marina*. Eelgrass has been utilized in many seagrass restorations (Fonseca et al. 1988). Recent losses of eelgrass and scallops in Long Island Sound due to a "brown tide" (Chris Smith pers. commun.[5]), and losses of scallops in Bogue and Back Sounds, Carteret County, NC, apparently due to a *Ptychodiscus* bloom, have prompted questions regarding seagrass and scallop restoration. Given the paucity of information on faunal recovery in restored or created seagrass beds,

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we sought to evaluate whether bay scallop, *Argopecten irradians*, stocking could be conducted simultaneously with eelgrass bed creation.

Under this approach, stocked adult bay scallops would be used as a source of spat settlement in the maturing eelgrass bed. Bay scallops often utilize eelgrass meadows throughout their life cycle (Gutsell 1930; Kirby-Smith 1970; Thayer and Stuart 1974). During the postveliger stage of development, a bay scallop attaches itself to submerged substrates such as vegetation (eelgrass blades), shells, rocks, animal tubes, or macroalgae. At approximately 10 mm in shell width, the scallop detaches and settles onto the bottom sediments to complete its life cycle; adult sizes range between 5 and 7 cm (Gutsell 1930; Kirby-Smith 1970; Thayer and Stuart 1974). During its lifespan (1.5–2 years), bay scallops feed upon phytoplankton (Peirson 1983) and detritus (Kirby-Smith and Barber 1974), which are plentiful in eelgrass systems (Thayer et al. 1975). If scallop stocking could not be done concomitantly with bed creation, natural recovery of the scallop population could be substantially delayed.

Our study was embedded in a larger, long-term study of eelgrass restoration and faunal recovery. In that study, eelgrass was transplanted onto subtidal dredge material and monitored to determine the rate at which these propagated areas attain functional characteristics of adjacent, natural meadows.

In preparing for the bay scallop stocking study, we observed in an independent scallop dredging survey that scallop densities near the study site declined from 2.0 to nearly 0/m^2 between November and January 1985. During this period, laughing gulls, *Larus atricilla*, were seen dropping live scallops, a common feeding activity for these birds (Pearson et al. 1959), onto a dredge material island adjacent to our study area. This suggests that the gulls were at least partially responsible for the observed decline in scallop densities. Because this portion of the study was designed to include an evaluation of developing eelgrass meadows as scallop habitat, the close proximity of the dredge island and the increased likelihood of high predation on the scallops by gulls had to be considered in the assessment. Given the decline in the natural scallop population, possibly exacerbated by gull predation, we utilized a mark and recapture technique to assess stocking feasibility.

The general objectives of the study were to compare the capabilities of natural eelgrass, transplanted eelgrass, and unplanted areas in supporting a stocked adult bay scallop population as a means of enhancing recovery of a local fishery. Specifically, we sought to 1) examine the feasibility of seeding adult scallops in newly transplanted eelgrass beds; 2) relate scallop density in experimental plots to a) the proximity of these plots to the dredge island and b) any preferential migration from the transplanted or unplanted areas to the adjacent, natural eelgrass beds; and 3) control for adult scallop recruitment by comparing the densities of naturally occurring scallops in natural and transplanted eelgrass beds of two spatial arrangements, as well as in unplanted plots within the study site.

METHODS

The study site (long. 76°32′W, lat. 34°40′N, Fig. 1) was located at the southern end of Core Sound and northwest of Cape Lookout, NC. Specifically, the experiment was conducted off the southwest side of a dredge material island in relatively shallow waters (0.15 m at low tide and 1.0 m at high tide). The island was originally created 10 years before the study with maintenance dredging deposits added every 2–3 years. The overall study site covered 4,556 m^2, which was divided into five separate blocks extending out from the island (Fig. 2). For this study on the scallops, only blocks 1, 3, and 5 were utilized. Each block contained five different experimental units which were 7.5 m on a side (56.25 m^2). An experimental unit was separated from adjacent units by a 7.5 m corridor. The five treatments for each experimental unit were as follows: 1) natural interior eelgrass (NI, ⩾15 from unvegetated substrate), 2) natural eelgrass bordering unvegetated substrate (NE), 3) low perimeter to area (LPA) eelgrass transplant arrangement (see below), 4) high perimeter to area (HPA) eelgrass transplant arrangement (see below), and 5) bare (B), unplanted dredge material. Although positioning of the two natural treatments were fixed, the other three treatments were randomly assigned to the remaining three experimental units within each block.

Each experimental unit contained eight plots (2.25 m^2), which were consecutively located around the perimeter of the experimental unit (Fig. 2). These eight plots were designated to accommodate eight faunal sampling periods for the parallel study of fishery habitat establishment. The two transplant arrangements had different perimeter to area ratios in order to examine the refuge value of large, unbroken seagrass cover versus patchy cover. The LPA treatments had eelgrass planting units throughout the 7.5 m × 7.5 m area, whereas HPA

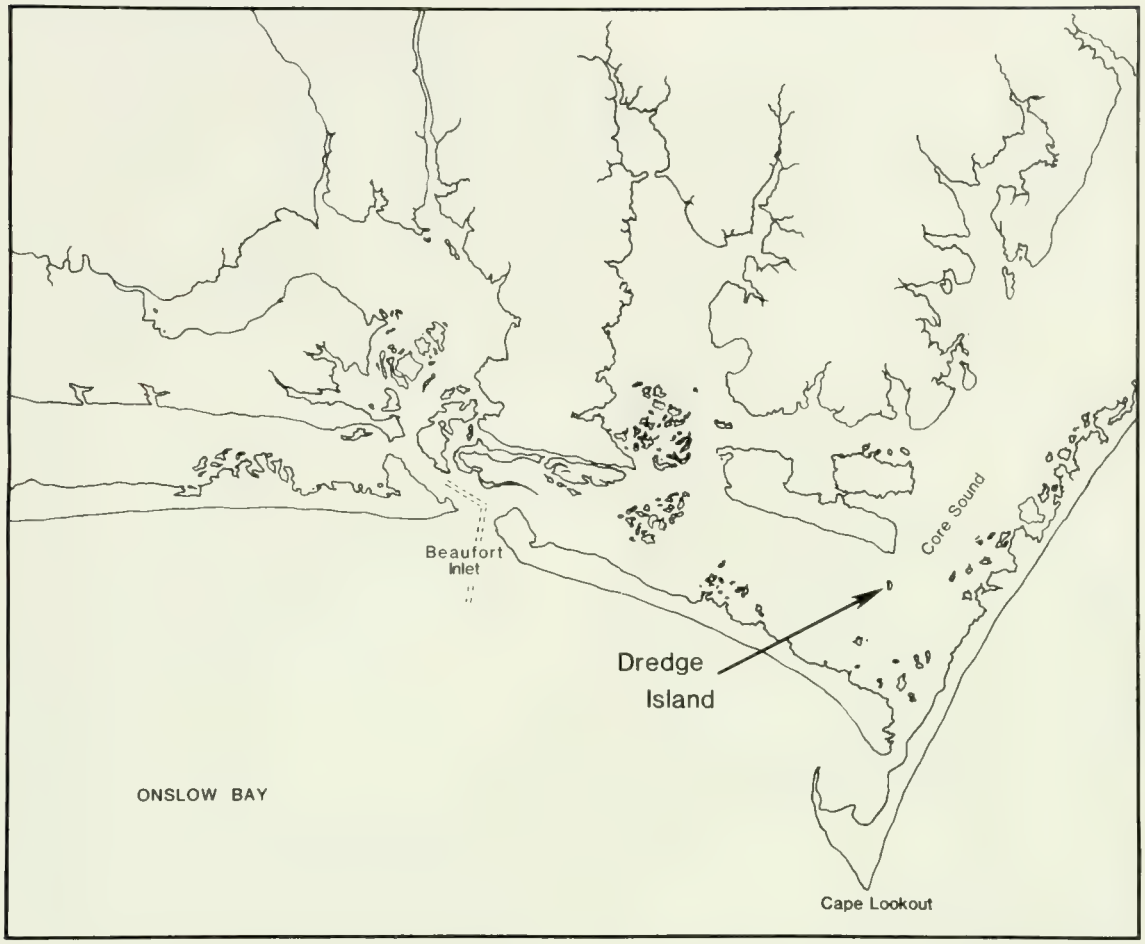


FIGURE 1.—An aerial view of Back Sound, North Carolina. Location of the study site and dredge island is long. 76°32'W, lat. 34°40'N.

treatments had 16 planting units on 0.5 m centers only within the eight 2.25 m^2 sampling plots. A planting unit consisted of 15 shoots of eelgrass tied together and anchored in the substrate with metal pins (Fonseca et al. 1985).

Eelgrass transplantation was performed in September 1985. Eelgrass cover, shoot addition, and seedling recruitment were monitored periodically in the transplanted treatments. Shoot density and cover in the natural meadow were monitored simultaneously with eelgrass seedling recruitment into unplanted areas by surveying randomly chosen plots within each treatment type. A 1.5 m × 1.5 m frame subdivided with cords into 36, 0.25 × 0.25 m (0.063 m^2) sections was laid down, marking the perimeter of the plots. In the natural meadow and unplanted areas, three randomly selected 0.063 m^2 sections were surveyed within each plot for the number of eelgrass shoots and seedlings. In transplanted plots, the intersections of alternate cords fell on the 16 eelgrass planting units per plot. Three of these were randomly chosen and the number of shoots and area of bottom covered were recorded for each planting unit. To obtain the coverage estimate, a smaller grid with cords on 5 cm intervals was placed over the planting, and the number of squares (0.0025 m^2) and half squares with eelgrass shoots were summed as area covered by the planting unit.

Bay scallops were collected from eelgrass beds to the southwest of the study site using a commercial scallop dredge and were held in tanks supplied with continuously flowing seawater. Seventy-five scallops (size range from umbo to lip, 6.0–7.5 cm) were marked with waterproof pens to denote the number of the individual and its block assignment. Additionally, we cut small notches in the shell ridges with

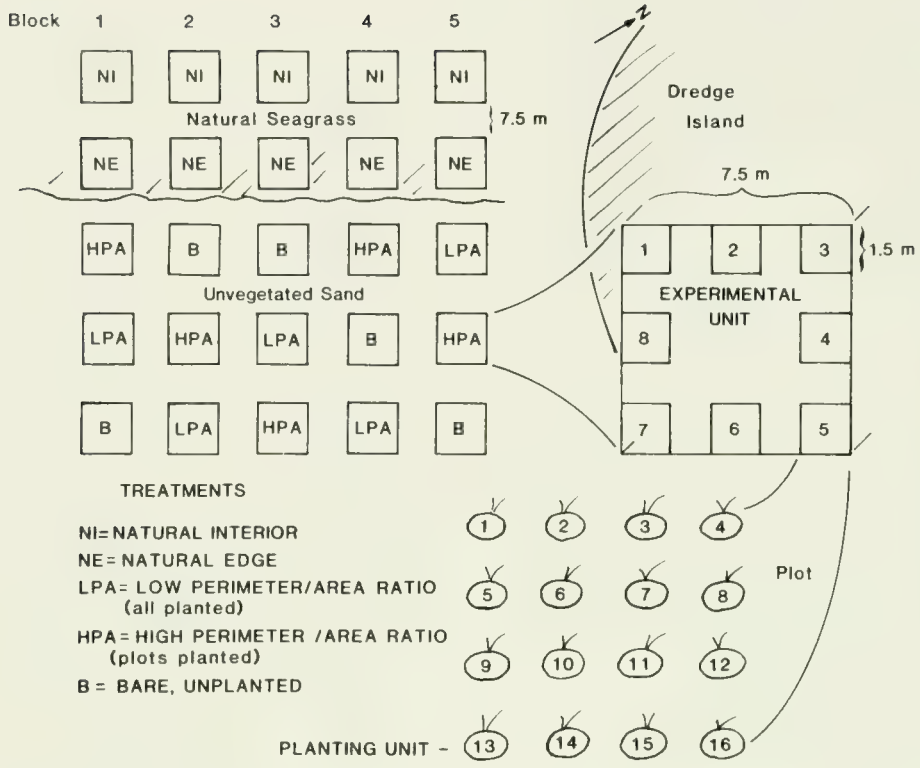


FIGURE 2.—Map view of the study site with the dredge island to the northeast. Each treatment is 7.5 m on a side and each plot is 1.5 m on a side.

a fine-tooth hacksaw blade to indicate the type of treatment.

The first placement of bay scallops was done during high tide on 20 February 1986. Based on natural scallop density surveys conducted in November 1985 showing densities of ~2.0 scallops/m^2, we stocked 5 bay scallops/2.25 m^2 plot. The 5 scallops were individually placed next to 5 randomly selected planting units out of the 16 in the plot. Thirty-four days after deployment, scallop surveys were conducted over four days from 26 to 30 March 1986 (survey I). The survey was conducted by placing a 7.5 m × 7.5 m grid made of ⅛″ nylon line, subdivided into 25 sections (2.25 m^2 each) over an experimental unit. Bay scallops were located by systematically searching the substrate and grasses by sight and touch while snorkeling. Within each 2.25 m^2 section, the efficiency of this method in recovering bay scallops <15 mm was untested, but recovery of bay scallops in the size range that was marked was 100% in three separate field trials. All unmarked bay scallops were measured to the nearest 0.1 cm on site, recorded by the section in which they were found, and replaced after measuring. Marked bay scallops were identified and recorded in the same manner.

Due to low recovery of marked bay scallops from the transplant and bare areas over the 34–38 d period, a second survey (survey II) was initiated which excluded the natural seagrass beds. This second set of scallops was identified with waterproof pens and notching, but both shells were notched in the event the shells became separated after death. Forty-five bay scallops, five in each of nine plots, were released in LPA, HPA, and B treatments in blocks 1, 3, and 5, but not in any natural treatments, on 30 March 1986 and surveyed 8 days later.

RESULTS

General observations during February through April revealed a variety of shorebirds, especially laughing gulls, brown pelicans (*Pelecanus occidentalis*), and cormorants (*Phalacrocorax olivaceus*), frequenting the dredge island. Seagulls dropped

mollusc shells onto the island repeatedly to fracture the shell and feed on the contents. A marked shell from the HPA treatment (survey II, block 1) was found in the intertidal zone of the island, and one from a natural edge plot in survey I was found at a high, central point on the island during a randomized search of the island. Other potential predators, blue crabs (*Callinectes* sp., $N = 3$) and whelks (*Busycon* sp., $N = 12$), also were observed in the grassbeds during the surveys.

Eelgrass cover and density in the natural meadow remained relatively constant throughout the study period. Natural bed experimental units had a consistent 77% cover, while shoot densities ranged between 441 and 1,148 shoots/m^2, with an average of 635 shoots/m^2 over the time between 20 February and 7 June 1986. Seedlings of eelgrass were observed among the natural and transplanted eelgrass in late March and early April. No eelgrass seedlings were recorded in the randomly chosen unplanted plots, although some were observed nearby. Throughout this time, transplanted treatments generally increased in number of shoots and area covered. By early June 1986, planting units averaged 0.02 m^2, or approximately 15 cm in diameter with an average of 25 shoots/planting unit.

After 34–38 days (survey I), 18 of 75 marked bay scallops (24%) were recovered (Fig. 3) and all were located in the plot in which they had been deployed. Fifteen of these 18 bay scallops were recovered in the natural grassbeds, with 9 located in the natural interior (NI) treatments and 6 in the natural edge (NE) treatments. Of the three remaining scallops, two were found in HPA treatments and one in a B, unplanted treatment. Three scallops were recovered from block 1 (farthest from the dredge island), 8 from block 3 (intermediate), and 7 from block 5 (closest).

A total of 207 unmarked, naturally occurring bay scallops were counted and measured during survey I (Fig. 4). There were 77 from the natural interior, 119 from the natural edge, 3 from LPA, 6 from HPA, and 2 from B, unplanted area treatments. One hundred and twenty-five bay scallops were found in block 1 (farthest from land), 50 in block 3, and 32 in block 5.

Our second, shorter survey recovered 10 out of the 45 (22%) bay scallops deployed in the transplanted grassbeds and B, unplanted areas (Fig. 3). Five of those recovered were located in LPA areas, 4 in HPA, and 1 in a B treatment. Five scallops were found in block 1, 2 in block 3, and 3 in block 5.

DISCUSSION

The greater recovery of marked as well as unmarked, naturally occurring bay scallops from the natural beds as compared to the transplanted and bare areas (Figs. 3, 4) indicated that natural bed treatments provided a more suitable habitat for adult bay scallops. Bay scallops in the transplanted areas apparently suffered a higher mortality than occurred in denser, natural vegetation as suggested by the low recovery of marked scallops and our observations of seabird predation. None of the bay scallops deployed in the transplants or bare areas were found in the natural beds, although in some instances the natural bed was only a few meters distant. The few scallops recovered from these transplant and bare treatments were found in the plot of their deployment. Either there was little movement of the deployed bay scallops, and they were preyed upon, or the ones that moved were preyed upon. Whichever the mechanism of loss, it was apparent that few survived the 34 d deployment in these treatments.

Neither treatment (LPA, HPA) of 5–6 mo old transplanted areas or bare areas provided the same habitat resource as adjacent, natural grassbeds (survey I); transplants did, however, provide a slightly better habitat for adult bay scallops than bare, unplanted areas over a short time (results from survey II). Twenty-two percent of the marked bay scallops were recovered from the transplant and bare treatments in survey II (8 day) deployment as opposed to 7% over the same area in survey I (34 days), suggesting a steady decline in numbers as a function of time. The extensive dense vegetation of the natural beds likely provides better refuge from predators such as gulls or blue crabs, along with increased protection from physically disruptive factors such as wave action.

Recovery of marked bay scallops from the treatment areas could not be attributed to the distance from the dredge island (Fig. 3). In survey I, the number of marked bay scallops recovered decreased with distance from the island, while in survey II, the opposite was observed. Distances from the island may not have been great enough to record a noticable difference in seabird predation upon adult bay scallops as a function of distance. The natural scallop population, however, did demonstrate a fivefold increase in numbers with increasing distance from the dredge island (Fig. 4). There is no bottom elevation gradient across this distance. Tidal flow and wave energy patterns around dredge island conceivably could interfere with recruitment of water-borne

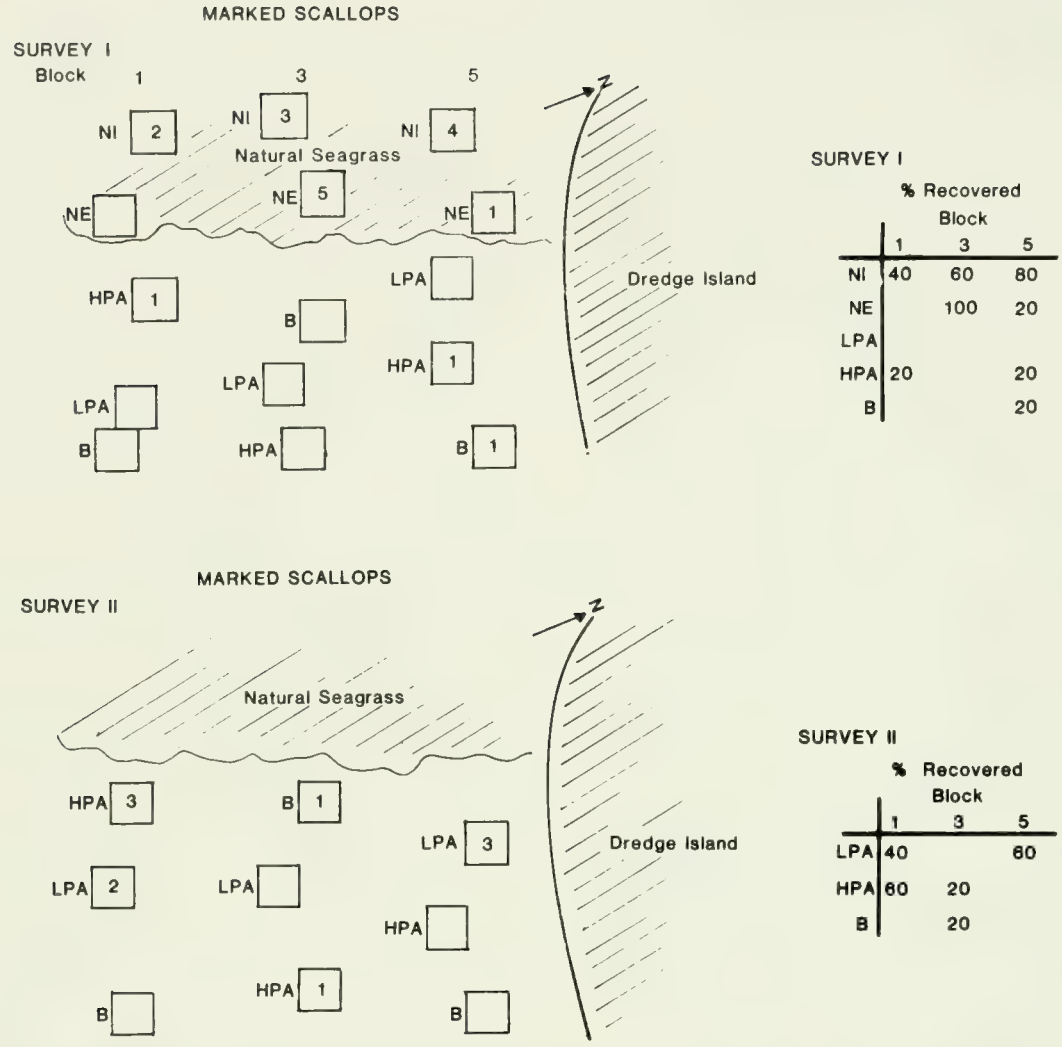
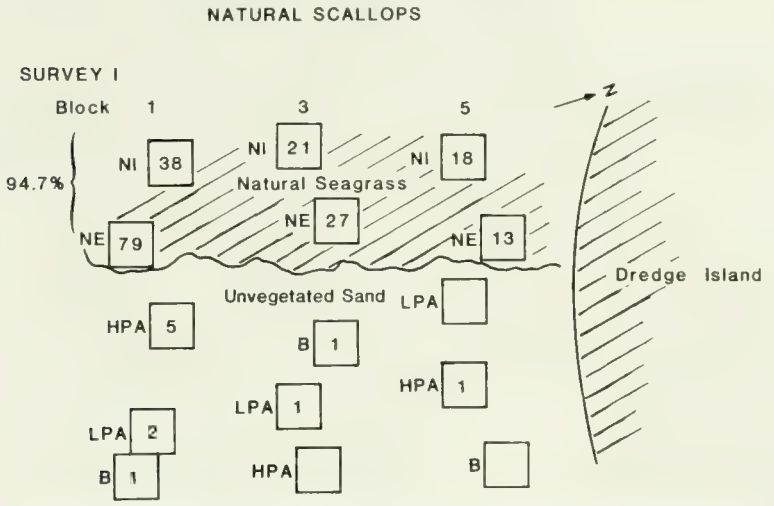


FIGURE 3.—Distribution of recovered scallops as numbers per experimental unit (survey 56.25 m^2). Survey I deployed 20 February 1986, and surveyed 30 March 1986. Survey II deployed 30 March 1986 and surveyed 7 April 1986. Five scallops were originally deployed in each plot. Treatment types: NI = Natural Interior, NE = Natural Edge, HPA = High Perimeter to Area, LPA = Low Perimeter to Area, B = Bare.

scallop larvae or diminish food sources closer to the island, making recruitment and feeding, not predation, a more likely factor influencing the existing natural scallop distribution.

Natural seeding of the eelgrass, together with the transplanted treatments, should gradually provide more protection for adult bay scallops and greater amounts of vegetative cover for postveliger scallop attachment, but this coverage will not occur within the first year using transplanted eelgrass (Fonseca et al. 1985). Since eelgrass must be transplanted in the fall in North Carolina (Fonseca et al. 1985), the eelgrass transplants during the first year, will not be of a size to provide habitat functions equivalent to natural beds when bay scallop larvae settle in the late winter. There is, therefore, a substantial time interval in which eelgrass transplants in this area do not have scallop habitat value equivalent to natural beds.

The creation of islands with dredge material in coastal waters may result in a reduction of bay scallop recruitment or survival within the area, as well as increasing bird predation by providing them with a substrate for dropping and opening scallops.



Natural Abundance

Treatment	# of Scallops
NI	77
NE	119
LPA	3
HPA	5
B	2

Block	# of Scallops
1	125
3	50
5	32

FIGURE 4.—Distribution of natural scallops as number per experimental unit survey (56.25 m^2) on 30 March 1986 (survey I). Treatment types: NI = Natural Interior: NE = Natural Edge, HPA = High Perimeter to Area, LPA = Low Perimeter to Area, B. = Bare.

Due to enhanced seabird predation, restoring eelgrass beds adjacent to these islands will likely not provide a suitable area for bay scallop stocking until the bed matures and coalesces. These results may not be widely applicable because our study focused on a single eelgrass-dredge island system over one scallop settlement season. However, it is apparent that the location and manner of dredge material disposal should be examined closely. Although shorebird and seabird habitat was certainly enhanced by the creation of the dredge material island, there may be local environmental and economic impacts on the scallop population and its fishery, as well as other existing, soft bottom communities, even without direct destruction of the adjoining seagrass bed itself as evidenced by the gradient of scallop abundance away from the island.

There are two major conclusions to be drawn from this study. First, if natural eelgrass meadows are destroyed and transplants are used as replacements for the lost habitat, it is essential to recognize that the transplants will not immediately function as the natural bed it replaced. The delay or lack of habitat replacement could permanently reduce the production of economically valuable fauna in the area if proper measures are not taken to insure that any removed or destroyed eelgrass is properly balanced with a functionally equivalent habitat replacement. Second, this study has shown that natural eelgrass beds at this site provided a substantially more suitable habitat for scallops than the transplanted treatments, within the first 5–6 months after planting. Stocking of recently transplanted eelgrass beds with scallops as a means of restoring or enhancing that fishery cannot be supported by these data.

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THE FOOD HABITS OF FIVE CRAB SPECIES AT PETTAQUAMSCUTT RIVER, RHODE ISLAND

JOHN W. ROPES[1]

ABSTRACT

The stomach contents of five crab species—green crab, *Carcinus maenas*; blue crab, *Callinectes sapidus*; lady crab, *Ovalipes ocellatus*; mud crab, *Neopanope texana*; and spider crab, *Libinia emarginata*—were examined from collections made in the Pettaquamscutt River, Rhode Island, during 1955–57. A carnivorous food habit characterized all species, although spider crabs contained plant foods more often than animal foods. Mollusks (especially pelecypods) and arthropods were frequent dietary components of the green, blue, and lady crabs. Intense predation on small, recently set pelecypods was indicated. The three species of portunid crabs (green, blue, and lady) appeared to have similar food habits, suggestive of potential interspecific competition for food. Crab remains were most frequently encountered in blue crab stomachs; lady crabs contained this food more often than green crabs. Small crustacea and plant foods occurred more often than hard-shelled foods and with equal frequency in the stomachs of small green crabs (<20 mm carapace width).

Predation by crabs has been identified as a serious threat to successful management of commercial bivalve resources (Carriker 1967; R. N. Hanks 1963; R. E. Hanks 1969). Many studies have concentrated on the green crab, *Carcinus maenas*, because of its abundance, its extensive distribution in the coastal zone of northeastern United States and Canada and Europe, and its predation on bivalves, especially the soft-shelled clam, *Mya arenaria*. Ropes (1968) and Welch (1968) have provided extensive reviews of the U.S. literature on this species; Davies (1966) and Kitching et al. (1959) have reported on its effects on European or blue mussel, *Mytilus edulis*, culture. Blue crabs, *Callinectes sapidus*; lady crabs, *Ovalipes ocellatus*; and mud crabs, *Neopanopeus texana*, have also been found to be predators of bivalves (Ryder 1884; Hay 1905; Fowler 1911; Belding 1930; Anon. 1941; Lunz 1947; Turner 1948; Bulter 1954; Landers 1954; Dunnington 1956; Darnell 1958, 1959; McDermott 1960; Galtsoff 1964; Loosanoff 1965). Many of these studies described the relationship between a particular predator and prey.

After completing collection and examination of green crab stomachs from Plum Island Sound, MA, I found that four of the species mentioned above and the spider crab, *Libinia emarginata*, could be collected from a fairly restricted area at the mouth of the Pettaquamscutt River, RI. This was an opportunity to examine possible inter- and intraspecific feeding habits by sympatric decapod crustaceans. The taxonomic relationship and morphological differences of the three portunid crabs (blue, green, and lady crabs) suggested making comparisons of stomach contents with each other and the two other crab species to determine the potential for predation on bivalves and to observe possible similarities and differences in their diets. The impact of such predation on bivalves of commercial importance has practical implications for resource management.

METHODS

From 1955 through 1957, crabs were collected during daylight hours from three subtidal areas of Pettaquamscutt River, RI, (Fig. 1) by towing a scallop dredge from a 12 ft aluminum boat powered by an 18 hp outboard motor (see Ropes [1968] for a description of the dredge). Intertidal areas were limited by the sharply sloping marsh banks which could not be sampled by the dredge. Thus, tows were made subtidally over shoal bars, along the edges of bars in the channel, and near the banks of the river. All samples were taken during ebb tide and before low water because experience at Plum Island Sound had shown that green crabs were actively moving about at that time. In 1955, five collection trips were made in July, September, and October; in 1956, six trips were made from May through August; and in 1957, nine trips were made in August through October (Table 1). At the laboratory, the species and

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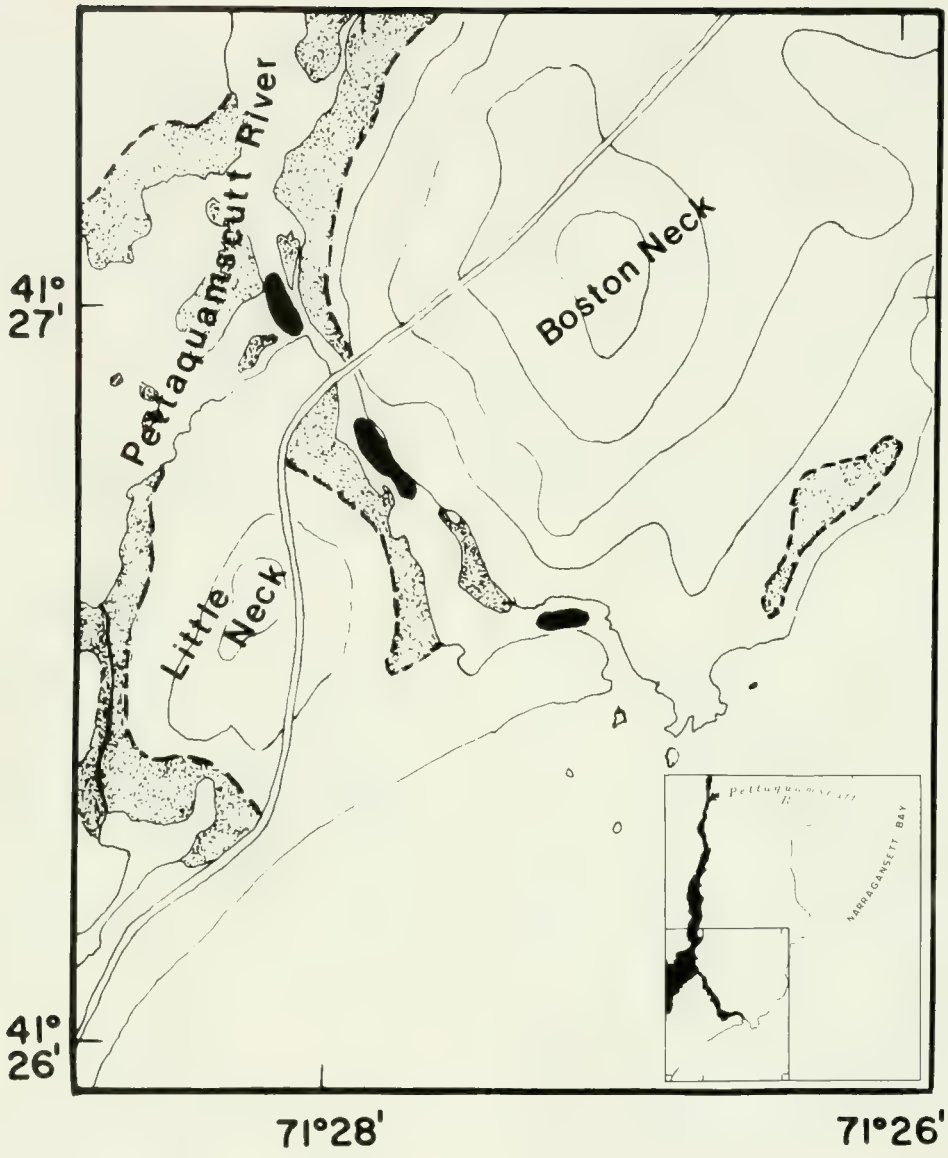

FIGURE 1.—Areas dredged (black areas) for crabs in Pettaquamscutt River, RI, 1955–57. Shoal bars were extensive near dredging areas. The islands were marshy (stippled areas) and were contiguous with mainland areas (dashed lines). An insert (bottom, right corner) shows Pettaquamscutt River in relation to the West Passage to Narragansett Bay.

sex of each crab were determined, and the carapace width (in mm) of each crab was measured with vernier calipers. Stomachs were then removed and preserved in 10% formalin. Food items were identified using a stereoscopic microscope, and the frequency of occurrence of each item was recorded. For some stomachs it was possible to count individual bivalves.

Descriptions of the amount of food in the stomachs were as follows: 1) full stomachs, containing tissues and hard parts of foods, 2) nearly empty stomachs, containing only a few fragments of hard parts of foods, and 3) empty stomachs. The stomachs in the first category were tabulated as the percentage of all crabs in a sample, and those in the second category as a percentage of the stomachs containing

TABLE 1.—Numbers of crabs caught in dredge tows at Pettaquamscutt River, RI, 1955–57.

Date	Number of tows	*Callinectes sapidus*	*Carcinus maenas*	*Ovalipes ocellatus*	*Neopanopeus texana*	*Libinia emarginata*
1955						
3 July	11	12	33	6	0	[1]1
6 Sept.	5	0	97	0	27	0
8 Sept.	9	14	26	14	8	0
3 Oct.	4	6	12	0	17	0
4 Oct.	4	0	18	0	0	0
1956						
2 May	4	0	16	0	0	0
4 June	7	0	25	2	0	[1]5
5 June	6	0	22	1	0	1
3 July	7	0	5	1	0	7
30 July	8	0	37	0	3	[1]6
29 Aug.	7	0	58	0	0	0
1957						
5 Aug.	3	14	[1]1	0	0	0
6 Aug.	3	30	[1]1	0	0	0
8 Aug.	3	19	0	0	0	0
15 Aug.	6	10	2	0	0	0
23 Aug.	5	62	24	1	0	3
4 Sept.	2	[1]2	20	0	[1]1	0
25 Sept.	4	19	27	5	0	7
14 Oct.	3	[1]2	29	0	0	0
31 Oct.	3	0	65	0	0	0

[1]Stomachs not examined.

food. Empty stomachs were omitted from all calculations.

Since most food consisted of crushed or fragmented remains, hard structures were relied upon for food identification. To assign a food to a definite species category was not always possible, but it could usually be included in a general taxonomic group. Thus, not all major taxonomic groups are the sum of specific items. Mollusk shells, and especially the hinge structure of pelecypods, could be most readily recognized. Annelids were identified by their jaws (whole worms were rarely found). Arthropods could rarely be identified to species, but were separated into three general groups: 1) crabs, which consisted of heavy pigmented exoskeletal remains, 2) small crustaceans, which consisted of translucent exoskeletal remains of amphipods, isopods, and small shrimp, and 3) barnacles (shells and bodies). Many stomachs contained food remains that were too fragmented or digested for identification. These were classified as unidentified remains.

Analysis of food habits by sex, molting condition, egg bearing, and mating were not possible due to the small numbers of each species collected. In a study of nearly 4,000 green crabs, Ropes (1968) found that feeding habits by sex were inconsistent and that feeding habits by premolt and very soft-shelled crabs (not included in the present study) were arrested. Similarly, ovigerous green crabs examined by Ropes (1968) tended to feed less than nonovigerous crabs, and the stomachs of mated pairs were nearly empty. Thus, analyses in the present study focused only on general food habits of the five species.

RESULTS

Although a few blue crabs were caught in 1955, none were taken in 1956 (Table 1). They were most numerous in the 1957 samples. The mean number per tow varied from 0 to 12.4. Green crabs were caught during every collection trip, except 8 August 1957, and were usually more numerous than the other crab species. The 6 September 1955 collection was unusual: 90 green crabs <10 mm CW (carapace width), 6 crabs <20 mm, and 1 crab 58 mm were caught entangled in decaying algae. It was the only collection containing such a large number of small-sized crabs. The mean number of green crabs caught per tow varied widely (0 to 21.7). Other crab species were caught infrequently and then in relatively low numbers.

Blue crabs ranged from 20 to 160 mm CW (Fig. 2). Although none exceeded 105 mm in 1955, 35% were larger in 1957. No size group was dominant; most ranged from 40 to 109 mm. Green crabs ranged from 4 to 70 mm, with most between 20

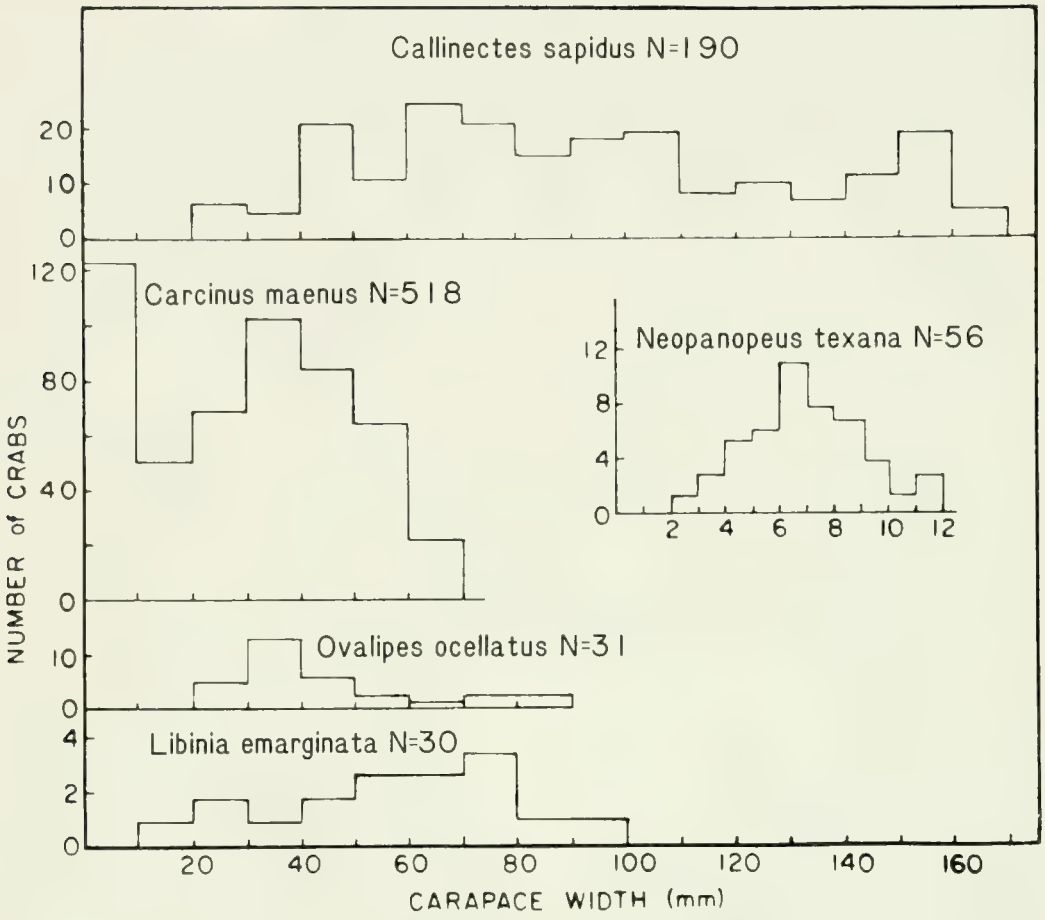

FIGURE 2.—Frequency distribution of carapace widths of five crab species collected from Pettaquamscutt River, RI, 1955–57.

and 59 mm. Lady crabs ranged from 27 to 83 mm CW, with most <50 mm. Spider crabs ranged from 13 to 93 mm and mud crabs from 3 to 12 mm.

Blue Crab

Animal foods were found in 91% of the blue crab stomachs and plant foods in 19% (Table 2). This indicated a predominantly carnivorous food habit. Of the animal foods, arthropods were more frequently (68%) encountered than mollusks (55%) or annelids (17%). Crabs (40%) and small crustaceans (33%) eaten by blue crabs were examined. Pelecypods (49%) were found more often than gastropods (12%), while the gem clam, *Gemma gemma*, (28%) and blue mussel (16%) occurred most often. The number of gem clams in 43 stomachs ranged from 2 to 821 (with an average of 66.8 per stomach). Few whole mussels had been eaten (≤4 per stomach), but most of them occurred as shell fragments. Other pelecypods found infrequently were soft-shelled and hard-shelled clams, and glossy shell (possibly *Tellina* sp.) and ribbed shell (possibly *Argopecten* sp.) fragments. Gastropods were found infrequently and, except for *Hydrobia* sp., were incomplete, broken shells or operculi. The jaws of *Nereis* sp. found in 13% of the stomachs indicated that it was the most frequently eaten annelid. Fish remains were found in 18% of the stomachs. Of the plant foods, *Spartina* occurred in 12% of the stomachs and algae in 8%. Unidentified tissues were in 67% of the stomachs. Although 75% of the blue crab stomachs contained food, 24% of these were nearly empty.

TABLE 2.—Occurrence and (percent frequency of occurrence) of foods eaten by five species of crabs collected in Pettaquamscutt River, RI, 1955–57.

Food items	*Callinectes sapidus*	*Carcinus maenas*	*Ovalipes ocellatus*	*Neopanopeus texana*	*Libinia emarginata*
Animal	126 (91)	240 (80)	17 (94)	16 (42)	5 (42)
Annelids	24 (17)	48 (16)	2 (11)	1 (3)	
Nereis sp.	18 (13)	37 (12)	2 (11)		
Other	1 (1)	3 (1)			
Mollusks	77 (55)	130 (43)	14 (78)	1 (3)	3 (25)
Pelecypods	68 (49)	92 (31)	13 (72)	1 (3)	3 (25)
Mytilus edulis	22 (16)	72 (24)	10 (56)	1 (3)	2 (17)
Gemma gemma	39 (28)	4 (1)	3 (17)		
Mercenaria mercenaria	3 (2)				
Mya arenaria	1 (1)				
Other		12 (4)	4 (22)		1 (8)
Gastropods	16 (12)	48 (16)	1 (6)		1 (8)
Hydrobia sp.	6 (4)	1 (1)			
Other	9 (7)	34 (11)	1 (6)		1 (8)
Arthropods	94 (68)	106 (35)	9 (50)	13 (34)	1 (8)
Crabs	55 (40)	11 (4)	5 (28)	1 (3)	1 (8)
Small crustaceans	46 (33)	75 (25)	3 (17)	12 (32)	1 (8)
Barnacles	1 (1)				
Foraminifera	2 (1)	20 (7)			
Fish	25 (18)	1 (1)		1 (3)	
Other					1 (8)
Plant	26 (19)	118 (39)		8 (21)	9 (75)
Algae	11 (8)	92 (31)		6 (16)	8 (67)
Spartina sp.	17 (12)	55 (18)		3 (8)	3 (25)
Unidentified	93 (67)	250 (83)	4 (22)	38 (100)	7 (58)
Stomachs with food	139 (75)	301 (71)	18 (58)	38 (69)	12 (67)
Stomachs nearly empty	33 (24)	50 (17)	1 (6)	3 (8)	3 (25)
Total number of crab stomachs examined	186	426	31	55	18

Green Crab

Animal foods were found in 80% of the green crab stomachs; plant foods occurred in 39% (Table 2). This indicated a predominantly carnivorous food habit with herbivorous tendencies. Of the animal foods, mollusks were found more frequently (43%) than arthropods (35%) or annelids (16%). Pelecypods (31%) occurred more often than gastropods (16%). Of the pelecypods, blue mussels were found most often (24%); gem clams and other pelecypods were infrequent food items. Other gastropods occurred most often (11%) as unidentifiable broken shells or operculi. The jaws of *Nereis* were found in 12% of the stomachs. Of the plant foods, *Spartina* was found in 31% of the stomachs, and algae in 18%. Unidentified tissues occurred in 83% of the stomachs. Although 71% of the green crab stomachs contained food, 17% of these were nearly empty.

Stomach analyses of small green crabs (<20 mm CW) caught on 6 September 1955 were sufficiently different to warrant separate representation (Table 3). Animal and plant foods occurred with equal frequency (69%) in the stomachs. Of the animal foods,

TABLE 3.—Occurrence and (percent frequency of occurrence) of foods eaten by small (<20 mm CW) green crabs caught on 6 September 1955.

Food item	Carapace width (mm) <10	Carapace width (mm) 10–19	Combined (Percent)
Animals	47 (70)	3 (60)	70 (69)
Annelids	1 (2)		1 (2)
Nereis sp.			
Other	1 (2)		1 (2)
Mollusks	1 (2)		1 (2)
Pelecypods	1 (2)		1 (2)
Mytilus edulis	1 (2)		1 (2)
Arthropods	43 (64)	3 (60)	46 (64)
Crabs	1 (2)		1 (2)
Small crustaceans	41 (61)	3 (60)	44 (61)
Foraminifera	1 (2)		(2)
Plants	46 (69)	4 (80)	50 (69)
Algae	44 (66)	4 (80)	48 (67)
Spartina sp.	2 (3)	1 (20)	3 (4)
Unidentified	25 (37)	3 (60)	28 (39)
Stomachs with food	67 (74)	5 (83)	72 (75)
Stomachs nearly empty	6 (8)		6 (6)
Total number of crab stomachs examined	90	6	96

arthropods were found most frequently (64%) and were predominantly (61%) small crustacean remains. The occurrence of the blue mussels, crab remains, and foraminifera in 2% of the stomachs indicated that these were minor dietary components. Algae was the dominant (69%) plant food; *Spartina* occurred in only 4% of the stomachs. Unidentified remains were found in 39% of the stomachs. Most stomachs (75%) contained food, although 6% of these were nearly empty.

Lady Crab

Animal foods were found in 94% of the lady crab stomachs; none contained plant foods (Table 2). This indicated a strictly carnivorous food habit. Of the animal foods, mollusks were encountered more often (78%) than arthropods (50%) or annelids (11%). Pelecypods occurred much more often (72%) than gastropods (6%). Blue mussels found in 56% of the stomachs were usually shell fragments; gem clams were found in 17% of the stomachs, and one stomach contained as many as 17. Other pelecypods found in 22% of the stomachs were glossy-white fragments (possibly *Tellina* sp.). Arthropod foods encountered were crab (28%) and small crustacean (17%) remains. The jaws of *Nereis* were found in 11% of the stomachs. Unidentified tissues occurred in 22% of the stomachs. Although 58% of the lady crab stomachs contained food, 6% of these were nearly empty.

Mud Crab

Animal foods were found in 42% of the mud crab stomachs; plant foods were in 21% (Table 2). This indicated a predominantly carnivorous food habit with herbivorous tendencies. Of the animal foods, arthropods were more frequently (34%) encountered than mollusks (3%) or annelids (3%). Small crustaceans were found in 32% of the stomachs, and crabs in 3%. Blue mussels were found in only 3% of the stomachs and none contained gastropods. Fish remains were found in only 3% of the stomachs. Of the plant foods, algae was found in 16% of the stomachs and *Spartina* in 8%. All of the stomachs with food contained unidentified tissues. Although 69% of the mud crab stomachs contained food, only 8% of these were nearly empty.

Spider Crab

Animal foods were found in 42% of the spider crab stomachs and plant foods in 75% (Table 2). This indicated a predominantly herbivorous food habit with carnivorous tendencies. Of the animal foods, mollusks occurred more often (25%) than arthropods (8%). Pelecypods were found more often (25%) than gastropods (8%). Blue mussels occurred in 17% of the stomachs. None of the stomachs contained annelids. Of the plant foods, algae was found in 67%, and *Spartina* was found in 25% of the stomachs. Unidentified tissues were found in 58% of the stomachs. Although 67% of the spider crab stomachs contained food, 25% of these were nearly empty.

DISCUSSION

Food habits of the five crab species were generally similar, a probable reflection of prey availability. Blue, green, and mud crabs tended to be carnivorous and spider crabs tended to be herbivorous, while lady crabs were observed to be exclusively carnivorous. However, neither of the latter two species was well represented (Table 2). Mollusks and arthropods were frequent dietary components of the blue and lady crab specimens (50% to 78%); such foods were in 43% and 35% of the green crab stomachs (Table 2). Many of the lady crabs (72%) and blue crabs (49%) contained pelecypods, but only 31% of the green crabs had eaten this food.

Green crabs are the sole portunid in the decapod fauna of Plum Island Sound, and Ropes (1968) found mollusks in 75% of the stomachs examined, with pelecypods (68%) the most frequent type of mollusk eaten. At Pettaquamscutt River, the low occurrence of pelecypods in green crab stomachs suggested that interaction between portunid species may have been affecting their feeding habits. Blue and lady crabs are adept at swimming and may use this ability in obtaining food and avoiding conflicts over food items; green crabs may be at a disadvantage in competing for food by their relatively poor swimming abilities. Many blue crabs were larger than the green or lady crabs taken, and their powerful claws may have been of positive advantage in encounters with other crabs. The high occurrence (40%) of crab remains in blue crab stomachs suggests inter- or intraspecific predation occurred, although the fragmented remains did not allow identification to species. Lady crabs may also have exerted predator pressure because 28% of their stomachs contained crab remains. Crab predation by green crabs was the lowest (4%) for the portunids examined and was lower than reported by Ropes (1968) at Plum Island Sound (13%).

Small green crabs caught on 6 September 1955

were almost equally carnivorous and herbivorous (Table 3). Relatively soft-shelled, small crustaceans (61%) and algae (67%) were found in the stomachs of green crabs; while only 2% of hard-shelled foods, such as pelecypods and crabs, were found. The mat of algae that entangled the crabs probably provided the foods seen in the stomachs and shelter from large predatory crabs and fishes. Ropes (1968) observed finger-sized holes, mats of algae, and *Spartina* high on the marsh banks of Plum Island Sound that were a refuge for small green crabs. This may be a means of circumventing cannibalism, because large green crabs typically occurred on the lower level clam flats during high tide and migrated to the subtidal zone during low tide. Ropes (1968) also found that soft foods, such as *Spartina* and algae, were important dietary components of small crabs. The omnivorous food habit and existence of small crabs in ecological niches apart from large predators has probable survival value.

Stomach analyses of the five crab species indicate that their food habits have probable important impact on the macrobenthic fauna of Pettaquamscutt River; these results support similar findings of other investigators of the food habits of crabs. The omnivorous food habit of the crabs has survival value, minimizing their dependency on particular food items. The carnivorous habit of blue, green, and lady crabs, which have a tendency to include many small pelecypods in their diet, suggests that recently settled pelecypods may be rapidly eliminated or severely reduced in numbers by predation. Clearly, a management scheme that minimizes the effects of crab predation on a bivalve fishery has a better potential for success.

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STOCK IDENTIFICATION OF WEAKFISH, *CYNOSCION REGALIS*, IN THE MIDDLE ATLANTIC REGION

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ABSTRACT

The hypothesis that a single stock of weakfish, *Cynoscion regalis*, existed in the Middle Atlantic was tested. Using starch gel electrophoresis we identified two polymorphic loci (6-phosphogluconate dehydrogenase and malate dehydrogenase) out of a total of 25 protein loci surveyed. Statistical analysis of allelic frequencies revealed that the populations were statistically indistinguishable.

Weakfish, *Cynoscion regalis*, commonly reach sizes between 70 and 80 cm in length and 3.0 and 4.5 kg in weight. They occur from Cape Cod, MA to Florida but are most common in the Middle Atlantic region (Wilk 1979). Weakfish participate in a spring spawning migration into bays and estuaries. In the fall, the migrations reverse and fish move either offshore or to more southern waters to overwinter (Welsh and Breder 1923; Bigelow and Schroeder 1953; Wilk 1979). Spawning occurs from May to mid-July in northern estuaries (e.g., Delaware Bay and Gardiners Bay, NY; Shepherd and Grimes 1984) and from March to September in more southern waters (e.g., North Carolina; Merriner 1976).

Weakfish are an important commercial and recreational species and historically landings have fluctuated widely. From 1940 to 1949, commercial landings averaged 8,800 metric tons (t), with a high of 18,800 t in 1945. Between 1950 and 1969, annual catches declined to an average of 2,600 t, but a resurgence occurred when the catches rose to a 7,700 t average between 1970 and 1979 (Wilk 1981).

Recreational landings of weakfish have been similarly variable, and in some years have been estimated to be as large as the commercial landings (Murawski 1977). In 1965, catches only amounted to 1,000 t but increased to 7,100 t in 1970 (Wilk 1981). In 1974, recreational landings were approximately 9,100 t, or about 60% of the estimated total catch (Murawski 1977). Landings dropped to 5,000 t in 1979, and Middle Atlantic states accounted for 95% of the catch (Wilk 1981).

Several studies (Nesbit 1954; Perlmutter et al. 1956; Seguin 1960) have concluded that there were multiple stocks of weakfish in the Middle Atlantic region based upon mark recapture, scale circuli spacing, and morphological data, respectively. More recent studies have shown geographic differences in growth and reproduction of weakfish between Cape Cod, MA and Cape Hatteras, NC (i.e., northern fish lived longer, grew larger, and had a lower relative fecundity than southern fish; Shepherd and Grimes 1983, 1984). These life history differences could be due to environmental effects or could be indicative of discrete stocks (Shepherd and Grimes 1983). We hypothesized that a single panmictic population of weakfish exists in the Middle Atlantic region. In order to test this hypothesis, starch gel electrophoresis was used to identify protein variation for two polymorphic structural loci (malate dehydrogenase-2 and 6-phosphogluconate dehydrogenase) found among weakfish in this region.

MATERIALS AND METHODS

We sampled adult and juvenile (young-of-year) weakfish along the east coast of the United States from Buzzards Bay, MA to Cape Hatteras, NC (Fig. 1). Adult fish were caught in the fall of 1982 and summer of 1983 by the National Marine Fisheries Service bottom trawl survey cruises (Grosslein 1969). We also purchased adults in some locations

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FIGURE 1.—Sampling localities of adult and juvenile weakfish sampled in the Middle Atlantic Region.

(i.e., Belford, NJ, the York River, VA and Cape Hatteras, NC) during the spring of 1982 and 1983.

We collected juvenile fish in their natal estuaries to minimize possible effects due to mixing after the fish migrated. Fish were trawled in Delaware Bay, NJ, Chesapeake Bay, VA, and Pamlico Sound, NC from August to October 1981 and 1982. We measured fish to the nearest mm total length (TL) and determined sex (when possible). Extracts of eye, liver, and skeletal muscle tissue were separately placed in centrifuge tubes and stored on dry ice. When this was not possible, we froze whole fish on ice and later removed the tissues in the laboratory. All tissue samples were stored at −8°C until analysis (for electrophoretic details see Crawford 1984).

Electromorph banding patterns were interpreted based upon the protein's subunit structure and previous studies with homologous enzymes. (Utter et al. 1974; Harris and Hopkinson 1976). We numbered loci from the anode to the cathode in ascending order. Allozymes were measured in millimeters relative to the most common homomeric electromorph which was designated 100 and numbered accordingly. The bands exhibited were consistent with reported information on their molecular structure (Manwell and Baker 1970). Allelic frequencies of polymorphic systems were calculated and examined for conformance to Hardy-Weinberg expectations (HWE) using Levene's (1949) method for small sample sizes ($N < 100$). For polymorphic loci that had null alleles the statistical procedures of (Speiss 1977) were followed to test for HWE. Sampling localities were compared by using a chi-square contingency test for haploid frequencies (Speiss 1977). We tested juvenile and adult allelic frequencies of polymorphic loci (excluding rare and null alleles) to determine whether significant differences in gene frequencies existed among 1) geographic location, 2) size/age (i.e., adults vs. juveniles) groups, and 3) sexes. Sampling locations were tested within regions, and if there were no significant differences among sampling locations, they were pooled. Pooled samples were then compared with all other regions to determine if there were regional differences. We calculated (averaged over the polymorphic loci) the genetic variation among the samples (F_{st}) (Hartl 1980). We obtained the percent polymorphic loci (common allele (p) < 0.950) and genetic distances (Nei 1972) using a BASIC computer program by Green (1979).

RESULTS

Weakfish from four populations (Long Island Sound, NY, Delaware Bay, NJ, York River, VA, and Cape Hatteras, NC) were initially screened by starch gel electrophoresis using 15 protein staining systems (Table 1) to identify polymorphic loci and calculate genetic distances. In samples obtained from other collecting localities only the polymorphic loci were evaluated.

The activity of the 15 enzyme (protein) staining systems was interpreted to reflect 25 structural loci of which only two (8%) were polymorphic, 6-phos-

TABLE 1.—Proteins and gel buffer-tissue combinations that provided the best resolution.

Protein systems	E.C.[1]	Tissue	Buffer	# of loci
Alcohol dehydrogenase	1.1.1.1	Liver	I	1
Aspartate aminotransferase	2.6.1.1	Muscle	IV	2
Esterase	3.1.1.1	Muscle	IV	2
α-Glycerophosphate dehydrogenase	1.1.1.8	Muscle	II	1
Glycerate dehydrogenase	1.1.1.29	Muscle	II	2
Isocitrate dehydrogenase	1.1.1.42	Muscle	I	1
Lactate dehydrogenase	1.1.1.27	Eye	II	3
Malate dehydrogenase	1.1.1.37	Muscle	I	3
Malic enzyme	1.1.1.40	Muscle	I	1
Muscle protein (nonspecific)		Muscle	II	3
Phosphoglucomutase	2.7.5.1	Eye	III	1
6-phosphogluconate dehydrogenase	1.1.1.44	Muscle	I	1
Phosphoglucose isomerase	5.3.1.9	Eye	III	2
Sorbitol dehydrogenase	1.1.1.14	Muscle	II	1
Xanthine dehydrogenase	1.2.3.2	Liver	IV	1

[1]Enzyme Commission number.
I - Aminopropyl, pH 6.0 (Clayton and Tretiak 1972)
II - Tris Citrate, pH 6.8 (Shaw and Prasad 1970).
III - Tris Versane Borate, pH 8.0 (Shaw and Prasad 1970)
IV - Ridgway, pH 8.5 (Ridgway et al. 1970).

phogluconate dehydrogenase (Pgd) and malate dehydrogenase (Mdh-2). In addition, three other loci—aspartate aminotransferase (Aat), phosphoglucose isomerase (Pgi), and xanthine dehydrogenase (Xdh)—exhibited rare alleles (i.e., common allele (p) > 0.950). Six-phosphogluconate dehydrogenase produced a single zone of allozyme activity on the starch gel that we interpreted as the product of a single gene locus. The heterozygotes displayed three bands which is typical of this molecule's dimeric structure (Manwell and Baker 1970). In weakfish, Pgd exhibited three alleles designated as 100, 98, and 96, a rare allele. Both juveniles and adults had similar frequencies of the most common allele (Table 2).

At the Mdh-2 locus, a dimeric protein product formed heteropolymers with the products of other Mdh loci. These heteropolymers occurred between the products of Mdh-1 and Mdh-2, and Mdh-1 and Mdh-3. The Mdh-2 locus was associated with liver, and the Mdh-3 locus is thought to be expressed in mitochondria (Thorne et al. 1963). This enzyme system also displayed a fourth isozyme band that migrated cathodally. This Mdh isozyme band is not reported in other similar studies and we do not know what protein loci it represented (Fig. 2). The Mdh-2 locus was polymorphic and exhibited four alleles: 103, 100, 97 (a rare allele) and a fourth null allele (*Mdh-2*(*N*)). Two fish homozygous for *Mdh-2*(*N*) were found. One was in a sample of juvenile fish from Spencer's Bay, NC and the other in an adult from Chesapeake Bay. The frequencies for the most common allele are found in Table 2. The uneven sample sizes (Table 2) occurred because of protein denaturation. The denatured samples indicated by streaks in the gels were excluded from analysis.

Allelic frequencies of three samples differed significantly from HWE for Mdh-2 (Table 2). This deviation reflected a deficiency in the number of heterozygotes which may have been due to the presence of the null allele (Selander 1970; Speiss 1977). We estimated null allele frequencies from the square root of the phenotype for Spencer's Bay (0.151) and Chesapeake Bay (0.146). Using the mean of the two values to estimate the null allele frequency for

TABLE 2.—Allelic frequencies of juvenile and adult fish for Pgd and Mdh including sample size, frequency of the most common allele and the standard error. All samples were collected in 1982 unless otherwise noted.

	Pgd(*100*)		*Mdh-2*(*100*)	
Location	*N*	Frequency (SE)	*N*	Frequency (SE)
Juveniles[1]				
Northern Region				
Buzzard's Bay and Long Island, NY	125	0.580(0.083)	98	0.576(0.041)
Sandy Hook, NJ	53	0.632(0.047)	47	0.617(0.050)
Delaware Bay, NJ (1981)	49	0.541(0.050)	46	0.511(0.052)**
Delaware Bay, NJ	91	0.527(0.037)	101	0.584(0.035)
Chesapeake Bay Region				
James R., VA	38	0.605(0.056)	48	0.510(0.051)***
York R., VA (1981)		—	47	0.543(0.073)
York R., VA	89	0.584(0.037)	67	0.612(0.060)
North Carolina Region				
Far Creek, NC (1981)	28	0.536(0.066)	38	0.645(0.055)*
Far Creek, NC	94	0.500(0.036)	98	0.602(0.035)
Spencer's Bay, NC	43	0.430(0.053)	45	0.547(0.052)
Wysocking Bay and Far Creek, NC	64	0.428(0.044)	63	0.571(0.044)
Adults[2]				
Northern Region				
Belford, NJ (1983)	11	0.636(0.103)	29	0.500(0.066)
Chesapeake Bay Region				
Virginia	121	0.620(0.044)	138	0.554(0.038)
Southern Region				
North Carolina	57	0.596(0.065)	59	0.636(0.063)

*HWE χ^2 0.05 = 3.841, df = 1.
**HWE χ^2 0.01 = 6.635, df = 1
***HWE χ^2 0.001 = 10.828, df = 1
[1]Geographic comparisons among regions of allelic frequencies for juveniles; χ^2 = 1.942, P > 0.05, df = 2 (Pgd), χ^2 = 2.268, P > 0.05, df = 2 (Mdh)
[2]Geographic comparisons among regions of allelic frequencies for adults; χ^2 = 0.566, P > 0.05, df = 2 (Pgd), χ^2 = 3.020, P > 0.05, df = 2 (Mdh).
+Represents a pooled sample, where samples <10 were combined.

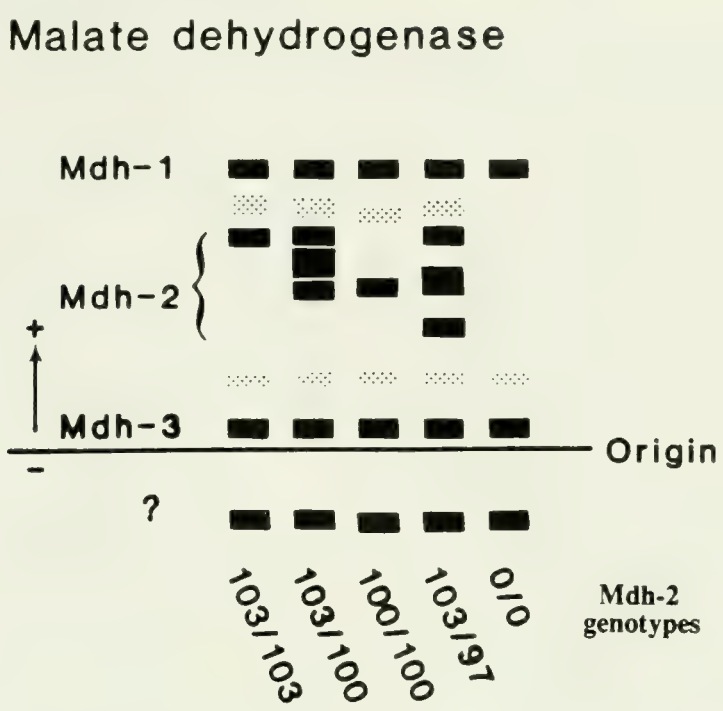

FIGURE 2.—Diagram of observed isozyme pattern for Mdh. The dark bands are protein products of presumptive loci and the lighter bands are heteropolymers formed from among the products of different loci.

localities that significantly deviated from HWE caused the chi-square values to become nonsignificant. At a frequency of 0.149 (if assumed throughout the sampling range) the expected number of individuals homozygous for the null allele among all the samples is 20, yet only two were found.

Our analyses indicated that there were no significant differences of allelic frequencies among sampling locations or among geographic regions (Table 2). The value of F_{st} was 0.046 and Nei's (1972) genetic distances were <0.003. No significant differences in allelic frequencies between juveniles (mean total length = 113 mm) and adults (mean total length = 310 mm) existed (Pgd: $\chi^2 = 2.622$, $P > 0.05$, df = 1; Mdh-2: $\chi^2 = 0.001$, $P > 0.05$, df = 1).

Comparisons between male and female fish indicated significantly different allozyme frequencies for Mdh-2 but not for Pgd. The frequency of the common allele (100) at the Mdh-2 locus was 0.518 ± 0.033 (SE) for 114 males and 0.637 ± 0.035 (SE) for 95 females, and these frequencies were significantly different ($\chi^2 = 6.024$, $P < 0.05$, df = 1). No differences were found at the Pgd locus ($\chi^2 = 1.785$, $P > 0.10$, df = 1).

DISCUSSION

Our study of allelic frequencies from populations of *C. regalis* along the east coast between Cape Cod, MA and Cape Hatteras, NC identified no statistically distinguishable differences. Nei's (1972) genetic distances are quite small and the F_{st} value (0.046) is low; both indicate little genetic variation among the populations. Nonsignificant allelic frequency comparisons among geographic locations and size/age classes were consistent with population homogeneity. A comparison of allelic frequencies at the Mdh-2 locus showed a significant difference between sexes. We are unable to explain this difference and cannot discount sex linkage or sexual selection as possible causes. Alternatively, with the numerous chi-square tests used in the analyses a Type II statistical error may have occurred.

Sample populations at several locations showed a heterozygote deficiency at Mdh-2 causing deviations from Hardy-Weinberg equilibrium. Several factors may cause heterozygote deficiencies (e.g., inbreeding, Wahlund effect, selection against heterozygotes, scoring biases, and null alleles; Speiss

1977), but the presence of null heterozygotes seems the most likely explanation. The low number of individuals observed to be homozygous for the null allele suggests that it may be lethal for these individuals (Speiss 1977).

Previous investigators have suggested that two or three distinct stocks of weakfish occur in the Middle Atlantic region (Nesbit 1954; Perlmutter et al. 1956; Seguin 1960). Nesbit (1954) examined distances between circuli on scales and conducted a marking study using celluloid belly tags. He tagged 5,789 fish and 7.5% were returned when the fish were eviscerated. Thirty-six percent of the returned tags were from retail dealers and consumers providing little information regarding actual recapture location. Nesbit concluded that the fishery consisted of two stocks. Perlmutter et al. (1956) examined intercirculi distances, fin rays, age, and growth data as well as Nesbit's (1954) data and concluded that there were northern and southern spawning weakfish populations.

Seguin (1960) performed a univariate analysis of morphometric and meristic data on juvenile weakfish and separated Middle Atlantic weakfish into three segments: 1) New York, 2) Delaware (and possibly Virginia), and 3) North Carolina. She reported "a north-south trend in regression coefficients" which may have been associated with environmental gradients (e.g., temperature) and clinal variation in the characters. Meristic characters, however, may be influenced by temperature (Barlow 1961) and intercirculi distances are related to growth rates that can vary geographically (Lux 1972; Shepherd and Grimes 1983; Harris and Grossman 1985). Because growth is affected by many environmental factors (e.g., temperature and food availability), it may not be indicative of genetic discontinuity (Joseph 1972).

Our results suggest that weakfish populations in the Middle Atlantic are not sufficiently distinct, genetically, to be considered as separate stocks (i.e., reproductively isolated). Weakfish perform extensive spring and fall migrations that could permit ample gene flow between populations. There are no obvious isolating mechanisms and only a small number of migrants would be needed to cause allelic frequencies to converge and make the population homogenous (Hartl 1980).

In conclusion, the results of this investigation do not support the findings of earlier studies that distinct stocks of weakfish are present in the Middle Atlantic. Even though there do not appear to be genetically discrete weakfish populations, there are variations in the population parameters (Shepherd and Grimes 1983, 1984). The ability of a population to sustain a harvest is largely dependent upon its growth, mortality, and fecundity. These life history parameters are used in fishery assessments (e.g., dynamic pool and stock-recruitment models). Use of northern weakfish growth parameters would predict overly optimistic yields for southern fisheries, and an incorrect stock-recruitment relationship. Therefore, as a practical matter it is probably best to manage weakfish as discrete northern and southern units. These units may not be reproductively independent, and the effects of fishing (particularly recruitment overfishing) are likely to be imposed upon the entire population.

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ESCAPEMENT BY FISHES FROM MIDWATER TRAWLS: A CASE STUDY USING LANTERNFISHES (PISCES: MYCTOPHIDAE)

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ABSTRACT

Escapement of fishes through the meshes of a trawl is a recognized but unquantified problem in estimating size of mesopelagic fish populations. This paper provides estimates of net escapement by midwater fishes, using the lanternfishes as an example. Comparison of overall catches for Tucker trawls of 1.6 mm and 4.0 mm mesh show highly significant differences. The small mesh size outcaught the large by a factor of 2.7 for fishes smaller than 30 mm SL, while for larger fishes, the small mesh catches averaged 90% of the larger mesh. Among six ranking abundant species, three patterns of escapement were observed, based on significant differences in cross-sectional fish dimensions and morphological characters: 1) The entire size range of the species was significantly underestimated (*Benthosema suborbitale* and *Notolychnus valdiviae*); 2) only size ranges below those of sexually mature adults were significantly underestimated (*Lampanyctus alatus* and *Lepidophanes guentheri*); 3) only juveniles <30 mm SL were significantly underestimated (*Ceratoscopelus townsendi* and *Diaphus dumerilii*). "Conventional" midwater trawl meshes of 4 to 6 mm diameter mesh provide adequate data for general distributional surveys and also for some quantitative estimations such as overall biomass. Determinations of juvenile biomass, spawning period, trophic impact, and relative species abundances based on conventional mesh collections may be prone to substantial error depending on species size. It is suggested that a net mesh of <2 mm be used in conjunction with larger mesh trawls if quantitative life history data on smaller size classes and species are required.

Requisite to studies of the roles of mesopelagic fishes in deep-sea ecological processes are accurate determinations of species composition and the vertical and horizontal structure of populations. Although these are now well documented for many groups in many regions of the world ocean (see Marshall 1980), accurate abundance estimates, particularly over the entire size range of a species, are often not possible because of sampling biases related to net construction and trawling methods (Stein 1985).

Two factors responsible for much of the difficulty in estimating abundance of midwater fishes are net avoidance by large size classes and escapement through the net meshes during capture by small fishes of slender body shapes (Harrisson 1967). Both result in underestimates of species abundance, which can apply to either particular size classes, or, in the case of diminutive species, an entire population.

While some studies show that net avoidance may be reduced through the use of trawls with large mouth areas, there are a number of attendant difficulties including enhanced escapement due to increased mesh size (Stein 1985). Of the two problems, net avoidance remains the most difficult to quantify. Escapement is more easily calculated, but little quantitative research has been directed towards this problem in studies of midwater fishes (Harrisson 1967; Clarke 1983a).

In this study we quantify escapement through net meshes of midwater trawls using the lanternfishes (family Myctophidae) as an example. The ecological implications of net escapement are discussed.

MATERIALS AND METHODS

Myctophids were collected during eight cruises aboard the RV *Suncoaster* from an area centered at lat. 27°N, long. 86°W. The cruises covered four seasons over a period of 30 months. Sampling months were September (1984), November (1985), January (1986, 1987), March (1985, 1987), May (1986), and July (1985). Station data are presented in Table 1.

All samples were taken using modified Tucker trawls fished open in an oblique "V" sweep from the surface to 200 m at night. This depth range encompasses the peak nighttime abundance of all

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numerically dominant lanternfish species in the eastern Gulf of Mexico (Gartner et al. 1987). All nets were fished at 1.5 to 2.5 knots with a total fishing duration for each sample of approximately 1 hour. Sampling usually began about 1 hour after sunset and ended 1 hour before sunrise. The bottom trawl bar was weighted to incline the net mouth about 30° from the vertical at these towing speeds (determined from observations using scuba). Two trawl configurations were used: a 5.3 m^2 (effective fishing area) net of 4 mm bar mesh in the body and 1 mm mesh in the funnel, and a 2.6 m^2 net of 1.6 mm mesh. Both nets had cod ends lined with 505 μm mesh.

Trawl depths were recorded by mechanical time-depth recorder (TDR) and monitored with an electronic deck readout linked to a transducer mounted on the trawl frame. The volume of water filtered during each net haul was calculated from flow meters mounted on the trawl frame.

Myctophids were fixed in 10% (v:v) formalin and preserved in 50% isopropanol. During all cruises except January and March 1987, a large number of postlarval specimens from the dominant species were removed from the catches for use in life history studies. These were blotted to remove excess moisture and measured to the nearest millimeter standard length (mm SL). The remaining myctophids were measured in the lab after preservation. Because of shrinkage of preserved specimens, the lengths of freshly measured individuals were decreased by 12% (shrinkage factor determined from Gartner, unpub. data; K. J. Sulak pers. commun.[3]). All myctophids were identified to the lowest possible taxon, with species identifications made using Nafpaktitis et al. (1977).

The effect of using nets of differing mouth areas was minimized by calculating the abundance of individuals per 10^4 m^3 for each net over the entire size range, which was then divided into 5 mm SL size classes. Kolmogorov-Smirnov (K-S) two-sample tests (Siegel 1956) were used for overall internet comparisons of capture over the size range by size classes and by net mesh for size groups smaller than 30 mm SL and larger than 30 mm SL. The K-S tests were applied to similar comparisons for each of the ranking myctophid species. Except where noted, the significance level for all tests was $P < 0.01$. Ranking species for all cruises were defined as the most abundant species which combined comprised 75% or more of the total number of specimens captured (Gartner et al. 1987).

To evaluate if escapement was related to body morphology as well as size, measurements of the greatest cross-sectional dimensions were made on a series of preserved specimens of each of the ranking species. Measurements were made to the nearest 0.01 mm using dial calipers on a series of randomly selected individuals which encompassed the postlarval size range of each species. Assuming that myctophids are elliptical in cross section, areas were calculated for each specimen using the formula πab, where a and b are the radii of the short and long axes of the ellipse. Cross-sectional areas were regressed against the square of length and tested for significance ($P < 0.01$) among species using a Student's t-test (Sokal and Rohlf 1981).

RESULTS

Collection Data

The 4 mm mesh net was used at 78 stations, from which 7,861 myctophids were collected with a total volume filtered of 1.65×10^6 m^3 (Table 1). The 1.6 mm mesh net was also used at 78 stations, with totals of 7,494 individuals captured and 8.97×10^5 m^3 filtered (Table 1). The mean ratio of volume filtered for the larger to smaller nets was 1.84:1 (range for all cruises was 1.72:1 to 2.07:1).

TABLE 1.—Collection data.

Cruise	Number of samples (Volume filtered 10^4 m^3)			
	3.2 m^2	1.6 mm	6.5 m^2	4 mm
September 1984	3	(3.84)	3	(6.42)
March 1985	14	(16.94)	11	(24.31)
July 1985	9	(10.28)	8	(17.56)
November 1985	4	(4.21)	17	(30.92)
January 1986	10	(11.85)	11	(26.13)
May 1986	13	(13.91)	10	(20.19)
January 1987	16	(18.89)	7	(16.32)
March 1987	9	(9.82)	11	(22.74)
Totals	78	(89.74)	78	(164.59)

Abundances by Size Class

The numbers of individuals collected per 10^4 m^3 for both nets are shown in Figure 1. Data for fishes larger than 80 mm SL were not included because only 16 specimens were collected. Catch differences were highly significant between the two mesh sizes ($P < 0.001$). In both nets, the 16 to 20 mm SL size class was most abundant, but the 1.6 mm mesh net

[3]K. J. Sulak, Atlantic Reference Centre, Huntsman Marine Laboratory, St. Andrews, New Brunswick, Canada E0G 2X0, pers. commun. May 1988.

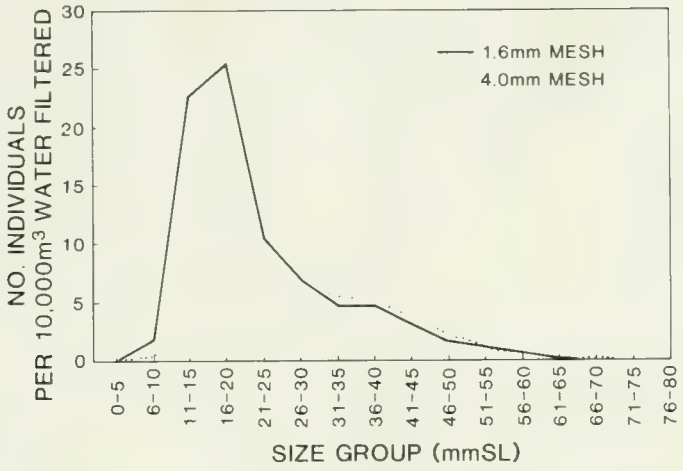

FIGURE 1.—Overall numbers of myctophids collected per $10^4 m^3$ water filtered for the 1.6 mm mesh and 4.0 mm mesh nets.

collected over twice as many specimens as the 4 mm mesh net. Overall, the 1.6 mm mesh net was significantly more effective in collecting individuals of smaller than 30 mm SL with a mean calculated abundance ratio for the 6 to 30 mm size groups of 2.7:1 between the 1.6 mm and 4 mm meshes. The abundance ratios for the small to large mesh sizes is highest for the smallest size group considered (4.4:1 for the 6 to 10 mm SL group).

Although the 4 mm mesh captured more fishes at sizes >30 mm SL, the differences, while significant, were not pronounced and never approached the ratios noted for the smaller size groups. The mean ratio for the 1.6 mm to 4 mm meshes for size groups 31 to 65 mm SL was 0.9:1 (range 0.8:1 to 1.0:1). At sizes larger than 65 mm SL, the ratios were variable owing to small sample sizes.

Abundances, Cross-Sectional Dimensions and Morphologies of Ranking Species

The same five species made up the ranking myctophids from both nets, although the order of abundance differed (Table 2). A sixth species, *Ceratoscopelus townsendi* (formerly *C. warmingii*, see Badcock and Araújo 1988), was also a dominant myctophid in the 4 mm net catches. Comparisons of internet abundances of ranking species for each size group revealed three basic patterns: 1) Virtually the entire size range was underestimated by the 4 mm mesh net (*Benthosema suborbitale* and *Notolychnus valdiviae*, Fig. 2a, b); 2) only size groups up to sexually mature adults (ca. 40 mm SL) were underestimated by the 4 mm mesh net (*Lampanyctus alatus* and *Lepidophanes guentheri* Fig. 2c, d); and 3) only juveniles smaller than 26 to 30 mm were underestimated by the 4 mm mesh net (*Ceratoscopelus townsendi* and *Diaphus dumerilii* Fig. 2e, f). Of the ranking species, only these last two species were collected in greater numbers by the 4 mm mesh net at sizes larger than 30 mm SL.

The patterns of net capture vs. size ranges were directly related to the general body dimensions and morphologies of the ranking species. Maximum cross-sectional depths and widths were measured on the body at the pectoral fin base in *Benthosema suborbitale*, *Lampanyctus alatus*, *Lepidophanes guentheri*, and *Notolychnus valdiviae*, while for *Ceratoscopelus townsendi* and *Diaphus dumerilii*, the maxima were on the head anterior to the opercular openings. Head profiles also differed among species, with the first four species having pointed or wedge shaped outlines, while the latter two had blunt, rounded heads. Both *N. valdiviae* and *B. suborbitale* (Pattern 1) are diminutive species not exceeding 22 mm and 33 mm, respectively, in the eastern Gulf, while the other four species grow much larger (Gartner et al. 1987; Gartner, unpub. data). Mean cross-sectional measurements (Table 3) show that in relation to body length, *B. suborbitale* is deep bodied, while *N. valdiviae*, *Lepidophanes guentheri*, and *Lampanyctus alatus* (Pattern 2) are all slender. When compared with the previous species at equivalent lengths, *C. townsendi* and *D. dumerilii* (Pattern 3) have generally thick cross-sections.

TABLE 2.—Ranking species of myctophids collected, by net.

Species	1.6 mm mesh Rank	No. captured	% of total captured	No./10^4 m^3	4.0 mm mesh Rank	No. captured	% of total captured	No./10^4 m^3
Notolychnus valdiviae	1	1,752	23.40	19.52	2	1,285	16.30	7.81
Diaphus dumerilii	2	1,317	17.60	14.68	1	1,572	20.00	9.55
Lampanyctus alatus	3	895	11.90	9.98	4	783	10.00	4.76
Lepidophanes guentheri	4	877	11.70	9.78	3	1,039	13.20	6.31
Benthosema suborbitale	5	778	10.40	8.67	6	597	7.60	3.63
Ceratoscopelus townsendi					5	645	8.20	3.92

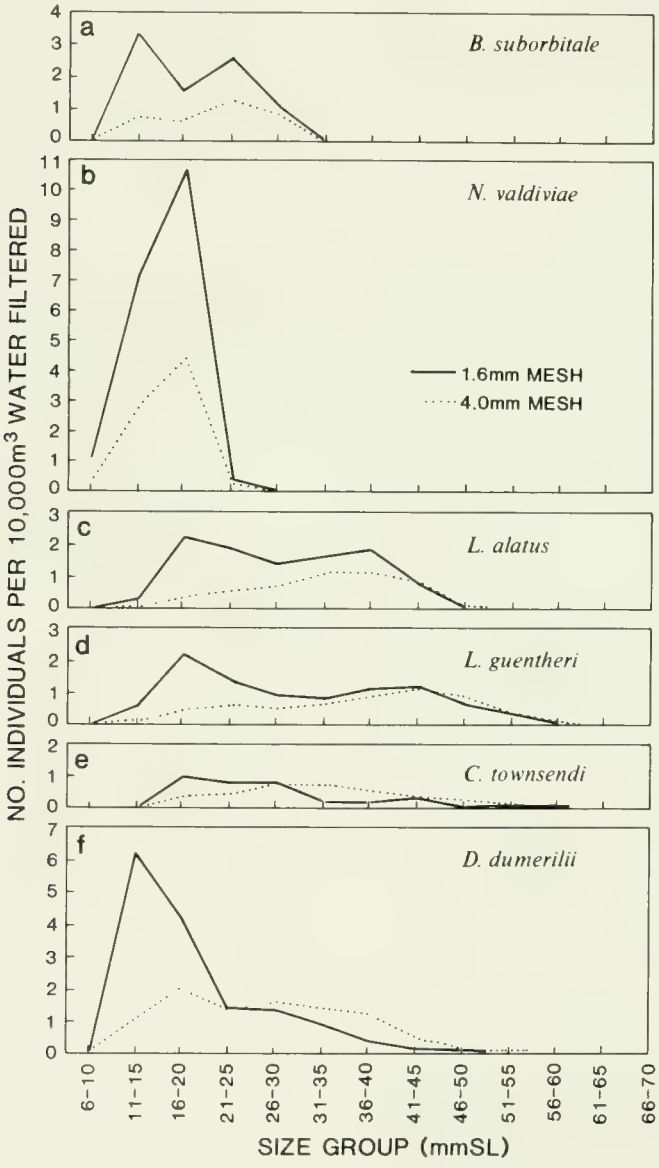

FIGURE 2.a–f.—Numbers of ranking species of myctophids collected per 10^4 m^3 water filtered for the 1.6 mm mesh and 4.0 mm mesh nets.

TABLE 3.—Mean cross-sectional dimensions (mm) and body morphologies for ranking myctophid species by size group. Underline indicates dimensions where number of individuals per 10^4 m^3 filtered are approximately equal between two net meshes (crossover point on Figure 2a–f). D = body depth (mm); W = body width (mm).

	Species									
	Benthosema suborbitale		*Ceratoscopelus townsendi*		*Diaphus dumerilii*		*Lampanyctus alatus*		*Lepidophanes guentheri*		*Notolychnus valdiviae*	
Head profile:	Pointed		Blunt		Blunt		Pointed		Pointed		Pointed	
Body morphology:	Deep		Thick		Thick		Slender		Slender		Slender	
Size class	D	W	D	W	D	W	D	W	D	W	D	W
8–10											1.72	1.14
11–15	3.05	1.43			2.69	1.49					2.06	1.42
16–20	4.52	2.30	3.51	1.87	3.58	1.83	3.09	1.56	2.76	1.44	2.80	1.74
21–25	5.70	3.02	4.75	2.60	5.03	2.54	3.90	2.14	3.85	1.77	3.26	2.10
26–30	6.41	3.34	5.74	3.34	5.95	3.03	4.85	2.45	4.76	2.36		
31–35	7.40	4.02	6.43	3.82	6.78	3.66	5.89	3.01	5.88	3.08		
36–40			7.56	4.41	7.61	4.24	6.77	3.43	6.87	3.64		
41–45			8.31	5.12	8.59	4.92	7.82	4.00	7.97	4.30		
46–50			9.21	6.14	9.59	5.71	8.35	4.18	8.27	4.43		
51–55			11.33	6.35	11.42	7.00			9.38	5.07		
56–60			11.75	7.46	12.57	7.88			10.24	5.21		
61–65									10.97	5.77		

The smallest size at which the 4 mm mesh net showed comparable catches to the 1.6 mm mesh for any ranking species was 23 mm SL (Fig. 2). Regression of cross-sectional areas vs. length for sizes larger than 23 mm clearly grouped the ranking species according to the catch patterns (Fig. 3). Differences between groups were highly significant ($P < 0.001$).

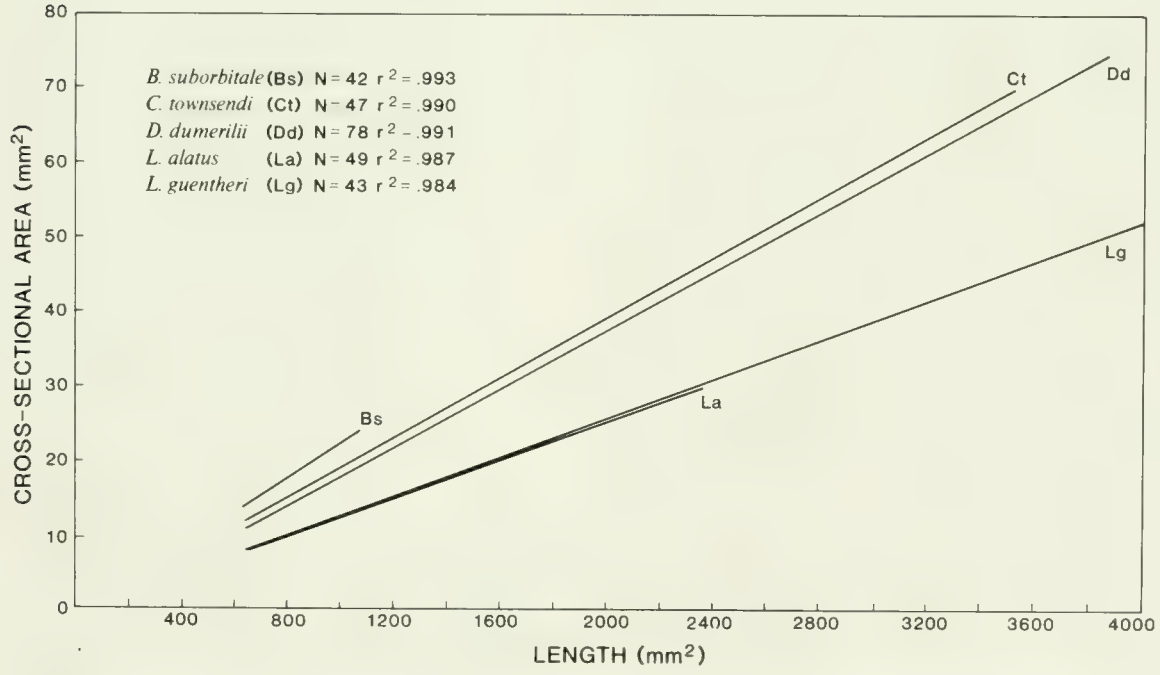

FIGURE 3.—Regressions of body cross-sectional area (mm^2) on the square of length for ranking species of myctophids (*Notolychnus valdiviae* excluded).

DISCUSSION

Net Escapement: Considerations

In the present study, the extent of bias due to net avoidance is unknown, but our trawling program was designed to minimize the problem as much as possible. All of our samples were taken at night when net avoidance is supposedly mitigated (e.g., Pearcy and Laurs 1966). Observations from submersibles suggest that small fishes (<60 to 70 mm) are not as successful in avoiding nets as are larger ones (B. H. Robison pers. commun.[4]). The myctophid faunas in low latitude ecosystems (upwelling regions excepted) tend towards the small end of the size range (Clarke 1973; Gartner et al. 1987). Also, the detection of nets by mechanical stimuli and the effective mouth area of a net have been suggested to enhance avoidance by midwater fishes (Harrisson 1967; Clarke 1973; Pearcy 1980; Stein 1985). Based on these factors, a smaller catch per unit volume would have been predicted for the 1.6 mm mesh net, which was white and had one-half the effective fishing area of the dark green 4 mm net. However, at size ranges smaller than 30 mm SL, it outcaught the larger mesh net by a factor of 2.7, whereas among larger fishes, it collected 80% to 97% ($\bar{x}$ = 90%) of the number of specimens of the large mesh.

Since the introduction of the Isaacs-Kidd midwater trawl (Isaacs and Kidd 1953), most midwater fish surveys have used gear with a net mesh size of 4 to 6 mm bar length (e.g., Badcock 1970; Hulley 1972; Clarke 1973; Gartner et al. 1987; Karnella 1987). While such gear is necessary for general surveys, our data suggest that they may be inadequate for obtaining certain quantitative estimates for small micronekton because of net escapement. It is clear that underestimates of myctophid abundance are marked in the 4 mm mesh (Figs. 1, 2). These underestimates may apply only to certain size ranges of the population, as in *D. dumerilii* or *L. guentheri*, or may include the entire size spectrum of a species, as in *N. valdiviae*. Similar trends of escapement have been noted among dominant species of sergestid shrimps examined from the same collections used in the present study (M. E. Flock pers. commun.[5]).

Many myctophid species, especially strong vertical migrators, are generally muscular and slender and possess very small teeth. They present a relatively small cross section that does not appear to be effectively retained by the large net meshes until some critical threshold of body thickness is reached. Among species with relatively pointed heads, i.e., those whose maximum body dimensions lie *behind* the head, the ability of large mesh nets to hold individuals is as much a function of the lateral thickness as it is of the dorsoventral dimension of the body. Even though dorsoventral thickness may greatly exceed mesh size, lateral measurements must be close to or exceed the mesh bar length in order for the 4 mm mesh net to sample these species as efficiently as the 1.6 mm mesh net (Table 3, Fig. 3). It appears that until both body axes are equal or greater in size than the mesh diameter, if a "pointed head" fish succeeds in getting its head through the mesh, it can readily escape. In contrast, species with maximum body dimensions *on* the head (blunt heads) show reduced escapement from the large mesh when the dorsoventral aspect alone reaches a critical threshold, i.e., they are not able to push their head through the mesh.

Implications of Escapement for Ecological Data

Collections of mesopelagic fishes from many regions are now extensive enough to provide a good representation of species composition and distribution, especially with respect to the families Myctophidae and Gonostomatidae (Gjösaeter and Kawaguchi 1980; Hulley 1981; Gartner et al. 1987, Karnella 1987). There has been increasing emphasis on quantitative assessment of various aspects of myctophid ecology, such as population dynamics (J. Gjösaeter 1973a, 1981; Clarke 1983b, 1984; Linkowski 1985; H. Gjösaeter 1987), trophodynamics (Clarke 1978, 1980; Baird and Hopkins 1981a, b; Hopkins and Baird 1981, 1985) and fishery potentials for midwater fish species (Gjösaeter and Kawaguchi 1980). In virtually all of these studies, data from mesh sizes of 4 mm or greater were used.

Our findings indicate that escapement among size classes and species smaller than 30 mm SL is pronounced and that midwater trawls with mesh of <2 mm diameter should be used in order to obtain accurate estimates of fishes in this size range. It is not enough to assume that catch efficiencies are proportional over all size ranges and that some factor can be applied to catches with larger mesh nets to account for escapement. It is clear that some species do appear to have proportional catch rates between

[4]B. H. Robison, Monterey Bay Aquarium Research Institute, 160 Central Avenue, Pacific Grove, CA 93940, pers. commun. June 1988.

[5]M. E. Flock, Department of Marine Science, University of South Florida, 140 Seventh Avenue S.E., St. Petersburg, FL 33701, pers. commun. June 1988.

the two mesh sizes, e.g., *Notolychnus valdiviae*, while others, e.g., *Lampanyctus alatus*, show very different catch rates depending on size group and mesh size (Fig. 2).

Overall biomass values for myctophids from the two mesh sizes are very similar, 19.61 g/10^4 m^3 (1.6 mm mesh) and 19.22 g/10^4 m^3 (4.0 mm mesh). This suggests that the larger mesh sizes provide a fairly accurate estimate of overall standing stock of myctophids and allow for interregional data comparisons (Maynard et al. 1975; Hopkins and Lancraft 1984). However, estimates of standing stock for certain size classes would be erroneous, especially for juveniles smaller than 30 mm SL (Fig. 4).

Net escapement by small size classes can also bias quantitative determinations of relative species abundance, spawning period, juvenile recruitment, and trophodynamic impact. *Benthosema suborbitale*, *Ceratoscopelus townsendi* and *Notolychnus valdiviae* are pan-oceanic in tropical-subtropical latitudes and are among the most abundant species throughout their zoogeographic range (Gartner et al. 1987). Based on our calculations, it is likely that *B. suborbitale* and *N. valdiviae* are of much greater numerical importance than previous data sets have suggested (e.g., Clarke 1973; Backus et al. 1977; Hulley 1981; Gartner et al. 1987).

Net escapement can also affect assessment of spawning period. Abundance comparisons for the two nets by cruise for *D. dumerilii* show that if one were to attempt to determine periods of larval recruitment for this species using length frequencies from the 4.0 mm mesh net, there are only suggestions of a spring-early summer spawning period (May 1986, July 1985), whereas the 1.6 mm net catches clearly indicate an early spring through fall influx of newly metamorphosed juveniles (Fig. 5). Using the small mesh net, the birthdays of juveniles for age and growth studies can more readily be fixed.

In trophodynamic studies that have considered the impact of midwater fishes on zooplankton prey, considerable predation pressure has been shown on certain size classes and taxa of zooplankters (Gjösaeter 1973b; Merrett and Roe 1974; Clarke 1978, 1980; Hopkins and Baird 1981, 1985; T. M. Lancraft pers. commun[6]; Hopkins and Gartner unpub. data). It is well documented that ontogenetic changes in prey taxa and size selection occur among myctophids. Our data suggest that predation pressure would be much higher from small size classes or species of myctophids <30 mm SL than could be calculated from studies using larger mesh collection gear.

CONCLUSIONS

As Harrisson (1967) remarked, no single midwater net will adequately sample all species or size ranges. At high latitudes and in the lower mesopelagic zone where many midwater fish species may attain sizes >100 mm SL, it has been observed that myctophids readily avoid even large midwater trawls (Pearcy

[6]T. M. Lancraft, Department of Marine Science, University of South Florida, 140 Seventh Avenue S.E., St. Petersburg, FL 33701, pers. commun. June 1988.

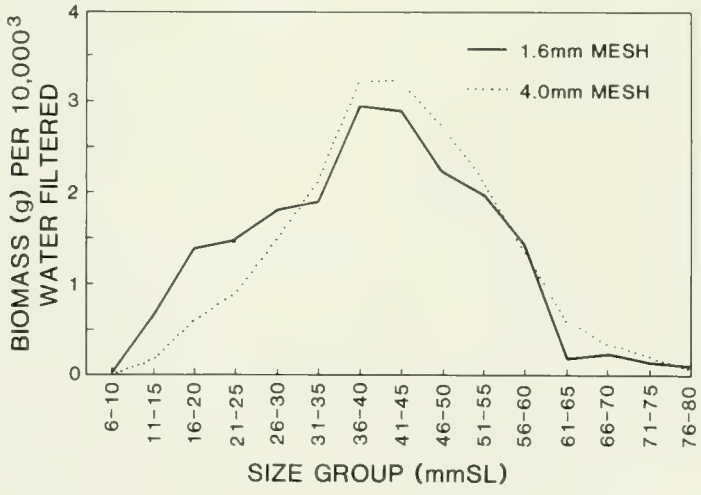

FIGURE 4.—Overall biomass of myctophids per 10^4 m^3 water filtered for the 1.6 mm mesh and 4.0 mm mesh nets.

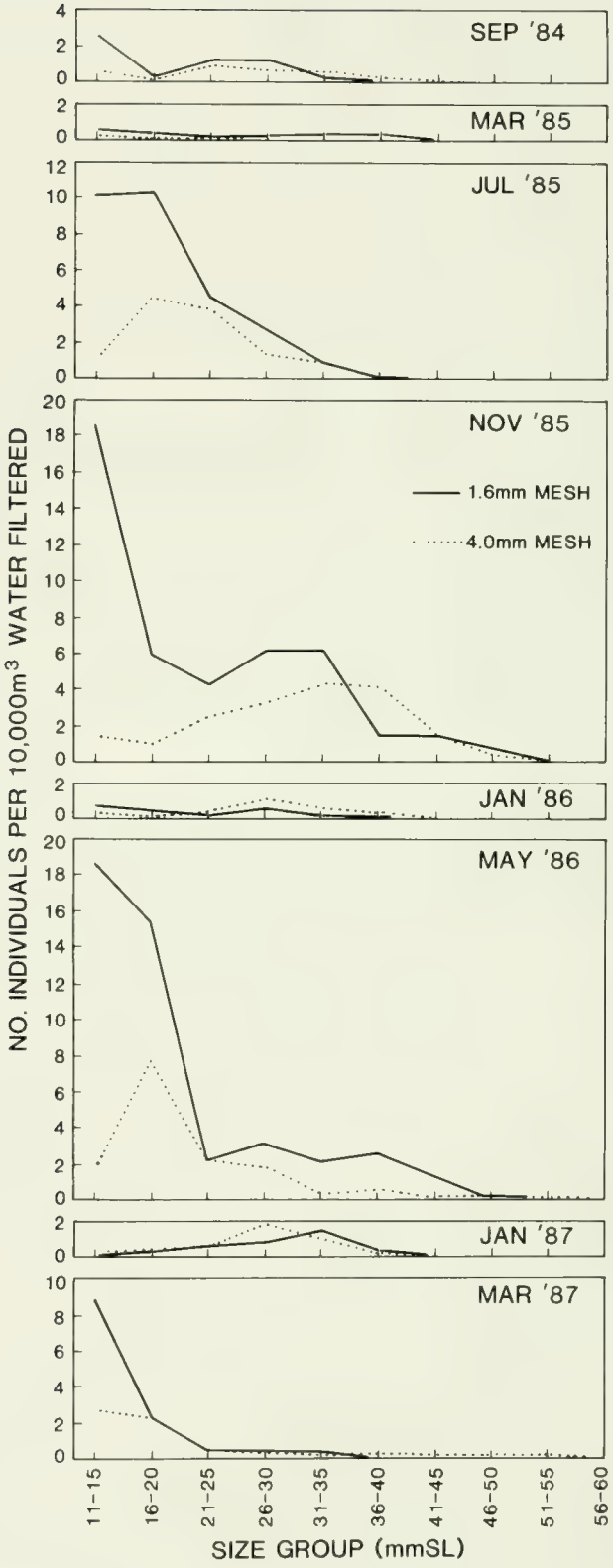

FIGURE 5.—Size frequencies of *Diaphus dumerilii* among collection periods.

and Laurs 1966; B. H. Robison, unpub. data from submersible observations). Our data and those of Clarke (1973) from conventional midwater trawls suggest that avoidance is not a primary concern in lower latitudes which are dominated by small (<70 mm SL) species. In all regions, however, escapement of small size groups and species through meshes is a real problem which until now has not been well quantified.

Future quantitative ecological research on postlarval midwater fishes should use a midwater trawl of mesh size <2 mm in conjunction with larger mesh in order to correct for the effects of net escapement. This ancillary net should ideally be mounted on an identical frame design (although not necessarily identical mouth area) as the large mesh and fished in a similar manner in order to readily facilitate internet comparisons. Should logistic considerations restrict gear use to a single type, our data indicate that the small mesh gear would be more efficient overall for collection of size groups from 10 to approximately 70 mm SL.

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THE ECONOMIC VALUE OF FISHING SUCCESS: AN APPLICATION OF SOCIOECONOMIC SURVEY DATA

RICHARD J. AGNELLO[1]

ABSTRACT

This paper focuses on an economic framework for analyzing some of the elements in the management of marine recreational fisheries. In addition, estimates are provided for valuing fishing success to marine anglers targeting on three Atlantic coast species: bluefish, summer flounder, and weakfish.

Demand functions for sport fishing are estimated with cross-section data using the travel cost method. Fishing trips per season are related to travel cost, fishing success, and income for individual fishermen. The marginal value of fishing success is determined using alternative models and estimation techniques. The data come from a one-time socioeconomic survey conducted by the National Marine Fisheries Service in 1981.

The findings show that marginal valuations for fishing success as measured by the number of fish kept by fishermen vary considerably among target species. In addition, these marginal values are quite sensitive to the empirical formulation of the model. The findings provide managers with some objective basis for evaluating policies affecting marine recreational fisheries. The wide range of values computed from the same data set, however, should caution us, and indicates the need for more theoretical and applied economic research in this area.

In order to efficiently manage marine recreational fisheries, information on economic valuations is required. Since recreational fisheries are typically in the nonmarket sector, traditional markets do not provide much direct information on recreational values in total or at the margin. As a result, management is hampered for recreational fisheries especially when attempting to evaluate activities which have potential effects on these fisheries.

In recent years, many studies have been performed to determine economic valuations of changes in several dimensions of recreational experiences. Examples from a variety of areas include water quality (Bouwes and Schneider 1979; Desvousges et al. 1983), congestion levels on beaches (McConnell 1977), and harvest rates for hunting (Miller and Hay 1981). For recreational fisheries, most studies traditionally have focused on freshwater sports fishing where the data base is generally stronger. Examples of empirical studies focusing on valuation of freshwater recreational fishing with emphasis on the importance of fishing success include Stevens (1966), Vaughan and Russell (1982), and Samples and Bishop (1985). In recent years, more attention has been directed towards saltwater recreational fisheries (examples include McConnell and Strand 1981 and Thompson and Huppert 1987).

Marine recreational fishing is particularly important because of its size and interactions with other sectors. It is estimated that more than 17 million marine anglers catch over 717 million pounds of fish and contribute over $7.5 billion dollars to the U.S. economy (U.S. Department of Commerce 1985). Although commercial marine harvests are considerably larger (6.3 billion pounds in 1985), conflicts between the two sectors are increasing and provide additional rationale for investigation into marine recreational valuation (Bishop and Samples 1980).

In this paper we focus on an economic framework for analyzing some of the crucial elements in managing marine recreational fisheries. In addition, findings are presented which provide an empirical basis for valuing fishing trips and fishing success to marine anglers targeting on three Atlantic coast species: bluefish, *Pomatomus saltatrix*; summer flounder, *Paralichthys dentatus*; and weakfish, *Cynoscion regalis*.

THEORETICAL BACKGROUND

The management of recreational fisheries would be enhanced if the value of the fishing experience and the impact of fishing effort on the resource base (and, hence, the future value of the fishing experience) were known. The former consideration involves measurement of economic demand which, for recreational fishing, can be complicated since mar-

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ket prices and quantities are generally not available. Even less well known is the impact that fishing effort (both past and present) has on the resource base and, hence, the current and future value of the fishing experience (e.g., quantity and average size of catch, crowding, etc.). Effects of stock externalities have been studied extensively for commercial fisheries and, although these externalities may exist for sport fisheries, little empirical evidence is available.[2]

We present an economic methodology for valuing recreational fishing assuming no stock externalities. Of particular interest is to separate the value of the quantity of fishing (e.g., the number of trips) from the value of the quality or success of the fishing experience (e.g., catch rate). Economic value can be derived from a demand relationship where the level or quantity (Q) demanded is related to price (P), income (I), and a vector of other relevant variables (S) including quality measures such as fishing success. The demand relationship is given as

$$Q = f(P, I, S), \quad (1)$$

where P, I, and S are treated as exogenous in the individual's demand or consumption level decision.

For recreational fishing, Q is usually measured as the number of fishing trips; P may reflect an entry price but more often is measured in terms of trip related costs; I reflects angler income (e.g., annual salary or hourly wage); and S reflects such things as fishing success and prices of substitute and complementary goods. Fishing success may be measured in terms of number and size of fish caught and/or kept.

The model is graphically presented in Figure 1 with quantity (Q) and price (P) on the horizontal and vertical axes respectively. The relationship between

[2]The stock externality results when increased fishing effort by individual participants affects the fish stock such that catch per day or average size of catch are adversely affected, and, hence, the value of a recreational fishing day for all participants is diminished. (Anderson 1983.)

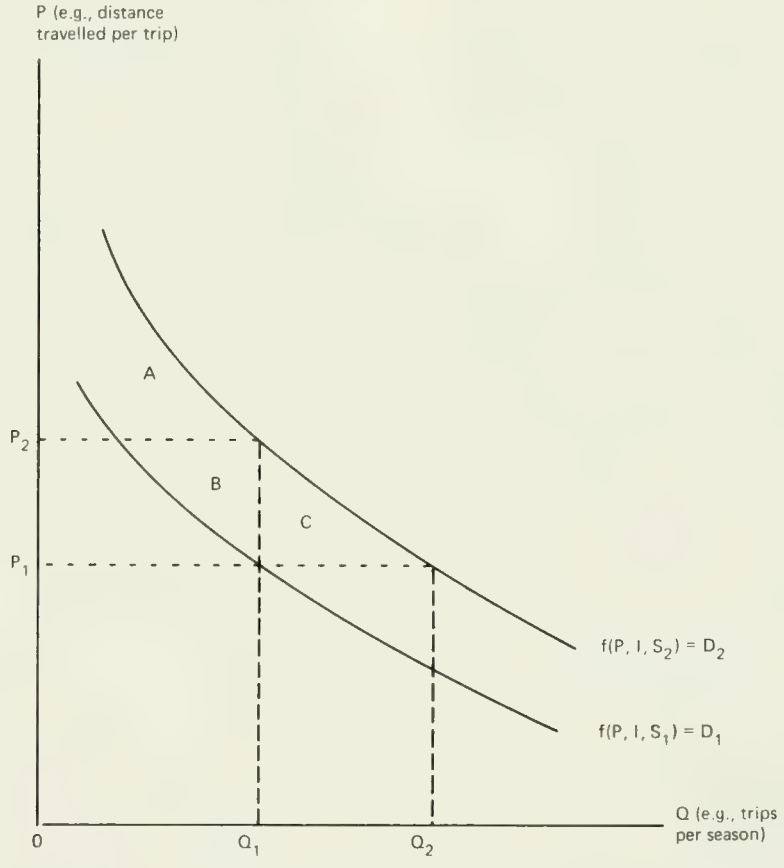

FIGURE 1.—Demand model relating travel frequency (Q) and cost (P).

Q and P is embodied in the slope of the curve. Relationships between Q and income (I) as well as other variables (S) can be shown as shifts in the demand curve. For simplicity and without loss of generality, let S represent single fishing success variable. For example, an increase in a relevant variable such as fishing success (S) from S_1 to S_2 is shown as a shift in the demand curve from D_1 to D_2 (i.e., from $f(P, I, S_1)$ to $f(P, I, S_2)$).

The value of an improvement in site quality, such as an increase in fishing success, can be measured in various ways. A common approach is to compare the areas under each demand curve and evaluate an increase in fishing success as a difference in the area over some quantity range (Freeman 1979). For example, let us assume that in a particular year or season an individual consumes Q_1 units at a price of P_1 when the level of fishing success is S_1 (i.e., reflected by demand curve D_1). Suppose the level of fishing success increases to S_2 (e.g., during the next year or season). Given the demand shift to D_2 and the old price of P_1, the individual would now consume Q_2. The economic valuation for the improvement in success or site quality totaled for the fishing season or year is approximately measured as the sum of areas A, B, and C. These areas represent an increase in consumer surplus for the fisherman experiencing an increase in fishing success and, thereby, increasing the fishing level from Q_1 to Q_2.

An alternative approach to valuation of fishing success is to measure the instantaneous (or marginal) change in welfare when fishing success changes (i.e., on a per-visit basis) rather than the accumulated gain over an entire season. This is the primary focus of our paper and can be accomplished in various ways. One approach is to convert the consumer surplus over an entire season into that of a single trip by dividing areas (A, B, C) by the number of trips per season. A more direct approach can be accomplished by first solving Equation (1) for P. For the moment, let us assume that Equation (1) is deterministic (i.e., nonstochastic) in nature and can be inverted mathematically. Thus we can solve for P as

$$P = g(Q, I, S). \tag{2}$$

Equation (2) is often referred to as the inverse demand function. The marginal value of fishing success $\partial P/\partial S$ can be measured as $\partial g/\partial S$ from Equation (2) where ∂/∂ represents the partial derivative operator. In Figure 1, this may be viewed as the distance $(P_2 - P_1)$ when the number of fishing trips is Q_1. This second approach will be the primary focus of the empirical analysis. It is more direct, has the advantage of less extrapolation from typical values of P and Q, and avoids any potential difficulty with an unbounded measure for area A arising with certain functional forms.

DATA

Since fishing trips and success are not commodities bought and sold in the marketplace, data are not readily available on P, Q, and S. As a result, survey methods are usually used to generate data on the number (Q) and price (P) of fishing trips and fishing success (S). The two most common survey approaches for relating Q, P, and S for individual fishermen have been 1) to directly ask marine anglers for valuation estimates of hypothetical changes in fishing trip frequency and success, or 2) to impute implicit valuation or trade-offs based on the various cost and activity level responses of a cross section of marine anglers. The first approach is usually referred to as contingent valuation and has been employed in fisheries valuation. Recent studies using contingent valuation surveys which attempt to incorporate catch rate and site information include Cameron and Huppert (in press) and Cameron and James (1987). The second approach using the travel cost method focusing on individual marine anglers will be used in this study. The travel cost method, although not without pitfalls, has been widely accepted as a means for valuing recreational resources when distance for fishing trips is well defined. An early implementation of the travel cost method can be found in Clawson (1959). For a recent summary of the travel cost method and its complexities, see Kealy and Bishop (1986).

The individual travel cost approach to evaluation relates travel cost and visitation frequency to recreational sites for individuals. This relationship provides an indirect way of observing how individual visitation frequency might respond to changes in an entry or purchase price as in a traditional economic demand relationship. Thus, behavior of marine anglers with respect to travel cost, travel frequency, and site quality (e.g., fishing success) provides the basis for estimating a demand equation for marine recreational fishing. The parameters of Equation (1) and/or (2) can be estimated using cross-section data on individual anglers.

In this study we are able to measure travel cost, travel frequency, success, and income variation for individuals from the Socioeconomic Survey conducted as a part of the Marine Recreational Fishery Statistics Survey (MRFSS) by the National Marine

Fishery Service (U.S. Department of Commerce 1981). Since in this study we wish to investigate the value of success by fish species, we chose samples of fishermen who preferred one of the three species of fish (bluefish, summer flounder, or weakfish). These species are of considerable importance to managers developing plans for fisheries along the Atlantic coast and are fairly similar with respect to mode, sites, and season. Since the number of observations for a given fishing site is generally quite low, and reduced further by focusing on specific fish species, pooling individual observations over sites was necessary in order to have enough interviews for statistical validity. Our sample sizes of anglers for bluefish, summer flounder, and weakfish are 270, 161, and 57 respectively and comprise sites from the Florida east coast to New York State. These data are pooled within a covariance statistical framework (i.e., with intercept and slope dummy variables) thus allowing the testing for differences across target species.

Although the survey contains a large and useful set of economic information on marine recreational fishing, the data provided are by no means ideal for an application of the travel cost method. Certain enhancements to the travel cost method could not be performed due to lack of data.[3] In addition, adjustments to travel distance and income were needed given the nature of the survey instrument.[4] The actual survey questions providing the data base can be found in Table 1.

A final point about the data base concerns the fishing success measure. Since trip frequency represents activity over the past year, ideally one would like a measure of fishing success to be reflective of the last year and thus reflect *ex ante* or expected fishing success. Unfortunately, the survey provides no longitudinal information on individual anglers. The measure of success is only for the day of the interview and may not have been typical and, therefore, inconsistent with the fisherman's past behavior.[5] We are forced to assume that *ex post* fishing success is a proxy variable for *ex ante* (expected) success. Travel frequency, distance, and fishing success thus reflect long-run equilibrium adjustment by the fishermen.[6] The empirical significance of fishing success reflects on both the importance of success to fishermen and the closeness of success realizations versus expectations.

EMPIRICAL MODEL

Trip demand for the ith fisherman is specified as a long-linear equation of either of the following forms:

$$\ln Q_i = b_0 + b_1 \ln P_i + b_2 \ln S_i + b_3 \ln I_i + bZ + e_i \quad (3)$$

$$\ln P_i = a_0 + a_1 \ln Q_i + a_2 \ln S_i + a_3 \ln I_i + aZ + v_i \quad (4)$$

where P, Q, S, I > 0; and

Q_i = the number of site-specific fishing trips (including the day of the survey) made in the last 12 months (Table 1, question 16),

P_i = round-trip cost in dollars to the site from either home or last night's accommodation (Table 1, question 18, as mod-

[3]Two refinements that are noteworthy, but could not be incorporated into the analysis due to the lack of data, include time costs and multiple site substitutions. It has been argued that time spent travelling as well as time spent at the recreational site reflects opportunity costs and should be included as part of the price of the fishing trip (Wilman 1980). The survey provides no information on travel nor visitation time.

Multiple fishing sites can provide an opportunity to construct prices for recreational substitutes and, thus, include these variables in the statistical estimation of the demand curve. See Samples and Bishop (1985) and Vaughn and Russell (1982). Unfortunately, no information on the angler's point of origin (e.g., ZIP code or area code) was available on the tabulated survey available to us so as to construct accurate distance (and price) measures for substitute sites.

[4]Since travel distance is a proxy for travel costs associated with fishing, travel distance from a permanent home to the fishing site might overstate travel costs for those individuals who were part-year residents of the area, vacationers, or on business. For part-time residents and those on business, the distance from last night's accommodation rather than home was used as the appropriate measure of travel distance. For vacationers, who comprised around one-sixth of the sample, one-half of the distance from home was used as their fishing travel cost.

Adjustments for the income variable included 1) assigning midrange values since respondents were asked for their income category rather as an actual dollar amount and 2) dealing with missing data since the income question appeared on a follow-up telephone survey for which the response rate was approximately half that of the field survey. Missing observations were handled by the zero-order approach whereby means replace missing values (Maddala 1977). Since income is an exogenous control variable and not central to the valuation calculations, these procedures were felt to be acceptable.

[5]An attempt was made to improve the success measure by focusing only on fishermen for whom the fishing success on the day of survey could be considered normal. This was done by utilizing a satisfaction level variable (Table 1, question 23) and eliminating those observations whose satisfaction was very high or very low. By eliminating those individuals with extreme satisfaction, it was felt that those individuals for whom the day's catch was not normal (or what was expected), would be eliminated from the sample. Unfortunately, the filter did not distinguish perfectly, and, in addition, reduced the sample to unacceptably low levels in part because satisfaction is measured on the follow-up telephone survey which had a lower response rate. The statistical results using this filter were less significant and, thus, the approach was abandoned.

[6]The implication of these potential errors in measurement is that the coefficient of success will be underestimated to a degree depending on the ratio of the variance of the error in measuring true success over the variance of observed success.

TABLE 1.—Survey questions used in the estimations.

From intercept survey

16. Including today's trip, about how many times would you say you have fished from [this (specify exact mode) in the last 12 months?/a (specify exact boat mode) leaving from this launching area in the last 12 months?]
18. To the nearest highway mile, about how far is it from your home to this fishing location?
29. May I look at the fish that you caught that you're taking with you? Enter species codes and number kept. Did you land any (specify common name) that you're not taking with you?
30. How many additional (specify common name) did you land?

From telephone survey

23. How satisfied were you with your fishing trip on (Month/Day)? Would you say you were

Very satisfied	(1)
Somewhat satisfied	(2)
Not too satisfied	(3)
Not at all satisfied	(4)

28. Finally, how much do you estimate that you personally earned in 1980 before taxes? Would that be

Less than $5,000	1
$5,000 to $10,000	2
$10,000 to $15,000	3
$15,000 to $25,000	4
$25,000 to $35,000	5
More than $35,000	6

(rescaled to 1987 dollars using the GNP price deflator).

ified in the above discussion,[7]

S_i = fishing success measured by the total number of fish kept (Table 1, question 29),

I_i = previous year's income of the respondent (Table 1, question 28), and

bZ, aZ = vector products of additive and multiplicative dummy variables and parameters allowing pooling across species to be tested using a covariance model (Kmenta 1986),

e_i, v_i = independent, identically distributed random errors.

The log linear specification is used since it provides a better fit over linear and semilog models in terms of t-statistics and the equation F-statistics. Recent studies estimating travel cost models have also found that log models provide better fits to the data. The choice of functional form has received much attention in the literature. Discussions of some of the issues including utility consistency, benefit sensitivity, and transformed parameter biases can be found in Bockstael et al. (1986), Stynes et al. (1986), and Ziemer et al. (1980).

Whether Equation (3) or Equation (4) is the appropriate model depends on the individual angler's choice process. If we assume that trip frequency (Q) is chosen after the site and thus travel cost (i.e., distance) is specified, Equation (3) is appropriate. If, on the other hand, anglers choose travel distance or cost (P) by choosing a recreational site after the frequency of visitation (i.e., the number of trips per year, Q) is determined, then Equation (4) is appropriate. Most likely both Q and P are endogenous to an individual angler so that ideally a multiequation model should be estimated that would include many competing sites as well as determinants of residential location choice. Unfortunately our data do not allow us to employ such a model.[8]

In our empirical analysis Equations (3) and (4) are estimated as single equation models and compared. Although Equation (3) is standard in the literature

[7]Dollar valuations are obtained by assuming a driving cost of $0.16 per mile. This figure reflects a rescaling to 1987 dollars of estimates appearing in "Cost of Owning and Operating Automobiles and Vans 1984," U.S. Department of Transportation, and includes only variable driving costs averaged over several vehicle types.

[8]Fishing success (S) also could be treated as an endogenous variable related to angler skill, experience, equipment, and the fish stock. An additional equation would be added to the model if one wished to "explain" S. The empirical approach would be affected depending on whether the model were simultaneous or recursive in nature. To the extent that fishing success (S) is related to travel frequency, Q (a proxy for experience), and travel cost, P, the model should be estimated as a simultaneous equation system. Unfortunately, additional variables required to adequately identify such a system are not available.

(e.g., see Kealy and Bishop 1986), our focus on marginal success valuations (i.e., $\partial P/\partial S$) makes Equation (4) more appropriate since no parameter transformations are necessary.[9]

Equations (3) and (4) were estimated first by ordinary least squares (OLS). Because the data are cross sectional on individual marine anglers, large variations in travel frequencies and cost exist which could lead to errors with unequal distributions. Various tests for heteroscedasticity were performed on the OLS residuals including Park, Glejser, and Bruesch-Pagan tests. The results were mixed with some tests indicating insignificant heteroscedasticity and some indicating significant (0.05 level, two-tailed) relationships between OLS residuals and travel cost (ln P) or travel frequency (ln Q) in Equations (3) and (4) respectively. Since the Glejser tests indicated the strongest relationship between the absolute OLS residual and the square root of ln P or ln Q in Equations (3) and (4) respectively, weighted least squares (WLS) was performed using $1/\sqrt{X}$ (i.e., where X is ln P or ln Q in Equations (3) and (4) respectively).

The results are found in Tables 2 and 3 for both OLS and WLS applied to the demand frequency (Q endogenous) and demand price (P endogenous models). The variables trip frequency (Q), trip cost (P), fishing success (S), and income (I) were defined

[9]Two statistical issues are relevant in the context of choice of dependent the variable: 1) The choice of dependent variable (e.g., ln Q or ln P) affects the regression slope unless the correlation (e.g., between ln Q and ln P) is perfect. Thus, estimating the ln Q relationship and solving for ln P generally yields a different estimate for ∂ ln P/∂ ln Q than estimating the ln P relationship directly. For a clear treatment of this point, see Wonnacott and Wonnacott (1979). 2) In addition, we note that parameter unbiasedness generally does not hold under nonlinear transformation although consistency does. Thus, partial effects on P using Equation (4) are potentially both unbiased and consistent whereas when using Equation (3) unbiasedness is lost for partial effects on P.

TABLE 2.—Log-linear demand frequency regressions (Equation 3). OLS = ordinary least squares; WLS = weighted least squares.

	Estimated coefficients (absolute t-values in parenthesis)					
	OLS			WLS		
Exogenous variable	(1)	(2)	(3)	(1)	(2)	(3)
Constant	1.930	1.970	1.792	2.383	2.421	2.833
	(2.17)	(2.22)	(1.59)	(2.54)	(2.57)	(2.21)
Log travel cost (P)	−0.173	−0.171	−0.181	−0.096	−0.096	−0.149
	(4.85)	(4.74)	(4.08)	(1.87)	(1.87)	(2.02)
Log fish kept (S)	0.050	0.048	0.074	0.034	0.034	0.055
	(3.13)	(3.05)	(3.53)	(2.28)	(2.25)	(2.72)
Log income (I)	−0.000	−0.005	0.020	−0.072	−0.075	−0.100
	(0.00)	(0.06)	(0.17)	(0.78)	(0.82)	(0.78)
Flounder (F)		−0.062	−0.124		−0.069	−1.799
		(0.44)	(0.06)		(0.51)	(0.91)
Weakfish (W)		0.290	1.966		0.182	0.622
		(1.29)	(0.49)		(0.85)	(0.16)
Interactions						
F and P (FP)			0.089			0.182
			(1.00)			(1.66)
F and S (FS)			−0.079			−0.071
			(2.22)			(2.15)
F and I (FI)			−0.031			0.112
			(0.16)			(0.58)
W and P (WP)			−0.100			−0.113
			(0.85)			(0.62)
W and S (WS)			−0.020			0.010
			(0.36)			(0.20)
W and I (WI)			−0.154			−0.012
			(0.39)			(0.03)
R^2	0.057	0.061	0.074	0.016	0.019	0.035
F (model)	9.71	6.28	3.45	2.66	1.86	1.56
F (species)[1]		1.03	1.08		0.74	1.31
n	488	488	488	488	488	488

[1]Computed from the formula $(\Delta R^2)(n\text{-k-1})/(1 - R^2)(r)$ where r, R^2, and $(n\text{-k-1})$ represent the number of restrictions, coefficient of determination, and degrees of freedom of the unrestricted model in hierarchial order (1), (2), and (3) respectively. See Wonnacott and Wonnacott 1979.

previously. The variables in the Z vector are defined in Tables 2 and 3. These variables reflect the additive and interactive (multiplicative) dummy variables which allow us to test for parameter differences across target species. Since the control group in all regressions is bluefish (i.e., anglers indicating bluefish as the species preference), qualitative (0,1) variables for flounder (F) and weakfish (W), along with their interactions with other exogenous variables are included in each regression. F tests (noted as F (species) in Table 2 and 3) were performed on the interaction and additive dummy variable terms. For the demand frequency regressions (Table 2), since the F (species) statistics for both the additive and multiplicative terms are insignificant, the data can be combined across target species. Thus, model (1) for both OLS and WLS are most appropriate when using Table 2). In the demand price regressions (Table 3), the species terms have significant F-statistics (to at least the 0.05 level) indicating that intercept and slope coefficients are different across species. Thus, models OLS (3) and WLS (3) are most appropriate from Table 3.

The empirical findings for the demand price model (Table 3) are stronger than for the demand frequency model (Table 2) although both have significant equation F-statistics (probability values < 0.05). WLS increases the significance of the results in Table 3 but lowers significance levels in Table 2. The parameter estimates for the travel cost and frequency coefficients (b_1 and $a_1 < 0$) as well as the success coefficients (b_2 and $a_2 > 0$) generally confirm theoretical expectations. Travel cost and frequency are significantly inversely related, and fishing success as measured by the number of fish kept is generally a significant determinant of both fishing frequency and travel distance. Various measures and combinations of fishing success were investigated,

TABLE 3.—Log-linear demand price regressions (Equation 4). OLS = ordinary least squares; WLS = weighted least squares.

	Estimated coefficients (absolute t-values in parenthesis)					
	OLS			WLS		
Exogenous variable	(1)	(2)	(3)	(1)	(2)	(3)
Constant	−0.310	−0.442	−1.892	0.372	0.225	−1.314
	(0.28)	(0.40)	(1.36)	(0.33)	(0.20)	(0.96)
Log trip frequency (Q)	−0.268	−0.261	0.289	−0.413	−0.393	−0.433
	(4.85)	(4.74)	(4.20)	(5.59)	(5.38)	(4.54)
Log fish kept (S)	0.087	0.089	0.113	0.088	0.095	0.135
	(4.45)	(4.59)	(4.45)	(4.32)	(4.72)	(5.23)
Log income (I)	0.260	0.253	0.408	0.228	0.215	0.388
	(2.37)	(2.32)	(2.97)	(2.04)	(1.95)	(2.87)
Flounder (F)		0.501	3.891		0.718	4.051
		(2.86)	(1.64)		(3.84)	(1.66)
Weakfish (W)		0.234	6.634		0.104	11.79
		(0.84)	(1.33)		(0.38)	(2.28)
Interactions						
F and P (FP)			0.182			0.243
			(1.47)			(1.55)
F and S (FS)			−0.027			−0.056
			(0.63)			(1.25)
F and I (FI)			−0.371			−0.404
			(1.58)			(1.68)
W and P (WP)			−0.316			−0.632
			(1.51)			(2.33)
W and S (WS)			−0.108			−0.144
			(1.57)			(2.10)
W and I (WI)			−0.600			−1.02
			(1.23)			(2.07)
R^2	0.087	0.103	0.126	0.097	0.125	0.164
F (model)	15.42	11.02	6.24	17.41	13.74	8.49
F (species)[1]		4.30	2.13		7.71	3.70
n	488	488	488	488	488	488

[1]Computed from the formula $(\Delta R^2)\ (n\text{-k-}1)/(1 - R^2)\ (r)$ where r, R^2, and $(n\text{-k-}1)$ represent the number of restrictions, coefficient of determination, and degrees of freedom of the unrestricted model in hierarchial order (1), (2), and (3).

including the number of fish caught as well as kept. These numbers were available in total as well as by species. Since the total number of fish kept consistently provided the best statistical fit, we report these results only.[10]

Our findings on income are mixed and appear to depend on the equation specification. While an important theoretical variable in most demand functions, we find that income is a significant positive determinant of travel cost but not travel frequency. Thus anglers with higher incomes travel greater distances but do not fish with greater frequency. This result is perhaps not surprising given the higher time opportunity cost for anglers with higher income. Our results for the lack of significant income effects on demand frequency are similar to findings in other studies (e.g., Vaughan and Russell 1982).

The coefficients for travel cost (P), frequency (Q), and success (S) in Tables 2 and 3 provide the basis for valuing fishing success. The valuation algorithm is outlined below using the instantaneous (marginal) approach discussed in the paper. Of particular interest is the measurement of the marginal value of fishing success ($\partial P/\partial S$) shown as ($P_2 - P_1$) in Figure 1).[11] We illustrate these calculations for summer flounder using the WLS model (3) results from Table 3. Since the regression slope coefficients reflect log derivatives (sometimes referred to as elasticities or price flexibilities), we begin by noting that

$$\frac{\partial \ln P}{\partial \ln S} = \frac{\partial P}{\partial S} \cdot \frac{S}{P}. \tag{5}$$

Solving this equation for $\partial P/\partial S$ provides a basis for valuing fishing success (S) using a log-linear model.

$$\frac{\partial P}{\partial S} = \frac{\partial \ln P}{\partial \ln S} \cdot \frac{P}{S}. \tag{6}$$

For summer flounder $\partial \ln P/\partial \ln S = (0.135 - 0.056) = 0.079$ which reflects the combination of the fish kept (S) term and the flounder and fish kept (FS) interaction term. Evaluating P and S at their sample means of \$50.61 and 1.94 respectively we obtain

$$\frac{\partial P}{\partial S} = 0.079\ (\$50.61/1.94) = \$2.06.$$

This number reflects the extra travel cost that a typical or representative fisherman is willing to incur in order to keep an additional fish per trip. In reality, since fishermen incur varying travel costs and experience a variety of success levels, the value of success is not unique.

Given that S in the calculation above was set at its mean for the entire sample, we refer to $\partial P/\partial S$ in this case as the marginal value of success for the typical fisherman (i.e., mean value). Alternatively, S can be set at different levels to obtain valuations other than at the mean since in a logarithmic model elasticities are constant but derivatives are not. For example, setting $S = 1$ we obtain a marginal value for the first fish kept of \$4.00, which is predictably higher than the marginal value of success evaluated at the mean (\$2.06). Since many fishermen catch one fish or even no fish, setting $S = 1$, although less reliable, does not reflect a large extrapolation. The logarithmic model allows us to observe the behavior of the value gradient for success across species and models.

In Table 4, marginal success valuations for all three species using various models (demand frequency and price) and statistical methods (OLS and WLS) are presented. The demand frequency results are based on the regression estimates from Table 2, models OLS (1) and WLS (1) since species pooling is appropriate. For the demand frequency results, different valuations are solely a reflection of alternative mean values of P and S across anglers preferring the various species. The combined valuation results reflect the weighted means of P and S across all anglers. The demand price results are based on the regression estimates from Table 3, models OLS (3) and WLS (3) because species pooling was not appropriate. Different valuations thus reflect both differences in regression coefficients as well as mean values of P and S. For comparison purposes with the demand frequency model, combined valuations in the case of the demand price model are based on the regression results of OLS (1) and WLS (1) in Table 3.

Although the absolute dollar values in Table 4 are subject to qualification, they do provide managers with numbers which can be compared across species as well as with market-determined commercial values. With the exception of the demand price models for weakfish where the combination of the

[10]The design of the survey may in part be responsible for the better fit with fish kept versus fish caught. Fishermen were asked to recall the number of fish landed, whereas the number kept were actually inspected by the interviewer (see Table 1, questions 29 and 30).

[11]We also note that by utilizing the marginal trip valuation algorithm outlined earlier rather than a consumer surplus integration calculation intercept estimates can be ignored. Thus, since only slopes are relevant there is not need to transform parameters by the factor $\exp(\sigma^2/2)$ in order to obtain unbiased mean rather median estimates (where σ^2 is the error variance; see Stynes et al. 1986).

TABLE 4.—Implicit marginal valuations of fishing success for Atlantic recreational anglers (1987 $). OLS = ordinary least squares; WLS = weighted least squares.

	Bluefish		Flounder		Weakfish		Combined	
Model	First	Mean	First	Mean	First	Mean	First	Mean
Demand frequency								
OLS	$4.66	$1.11	$14.63	$7.54	$4.89	$1.46	$7.98	$2.38
WLS	5.71	1.36	17.73	9.24	5.99	1.79	9.77	2.92
Demand price								
OLS	1.82	0.43	4.35	2.24	0.10	0.03	2.40	0.72
WLS	2.18	0.52	4.00	2.06	(1)	(1)	2.43	0.73
Means								
Travel cost	$16.14		$50.61		$16.93		$27.61	
Number of fish kept	4.20		1.94		3.35		3.35	

[1]Not computed since the net coefficient of log of fish kept for weakfish from Table 3 (WLS model (3)) was negative.

S slope coefficients and the WS interaction coefficients from Table 3 (OLS (3) and WLS (3)) resulted in either very small positive or negative values, the valuations in Table 4 provide us with interesting comparisons. Disaggregating the analysis by species appears to make a substantial difference. Recreational fishermen placed the highest valuation on summer flounder when compared with bluefish and weakfish. This holds regardless of whether one focuses on the first fish or the average number of fish kept. Generally, the value of fish kept at the mean level of success is between 1/2 and 1/4 that of the first fish. In our log-linear model, this diminishing valuation gradient is simply of function of the average number of fish kept. Thus, for summer flounder anglers where the average number of fish kept is 1.94, the value of the average fish is 1/1.94 that of the first fish. For bluefish and weakfish anglers, the value of the average fish is 1/4.2 and 1/3.35 that of the first fish respectively.

The demand specification appears to matter at least as much as species preferred when valuing success. The demand price model consistently generates significantly lower valuations than the demand frequency approach. As discussed earlier, the demand price model may be more appropriate since travel cost (P) is treated as endogenous, and thus the equation need not be inverted to find effects on price (i.e., $\partial P/\partial S$). For comparison with studies of freshwater fishing using a demand frequency approach, we note that Samples and Bishop (1985) found a value of $6.75 for an additional lake trout or salmon landed, while Vaughan and Russell (1985) found marginal values of $0.45 and $0.31 for trout and catfish anglers respectively. Our results for valuing fishing success offer some comparability with their findings and support the hypothesis that marginal valuations can vary greatly by species and by study. What is especially noteworthy is that success valuations can also vary dramatically by model specification within a species and study (i.e., for the same data set). In our study the method of estimation (i.e., OLS vs. WLS) has little effect on the parameter estimates of their significance levels. In general to the extent that the weighting procedure is appropriate, WLS provides a more accurate picture of reliability.

CONCLUSIONS

In this paper we have presented a theoretical and empirical economic framework for valuing fishing success of marine recreational anglers. The empirical analysis reveals that the number of fish kept by Atlantic marine anglers is generally associated with positive and significant dollar valuations. Sports fishermen implicitly reveal substantial variation in willingness to pay for catching and keeping Atlantic bluefish, summer flounder, and weakfish. These valuations also vary considerably by empirical model and the average level of success. Management policies aimed at promoting catch success have a stronger empirical basis for measuring the benefits of increased catch and comparing these benefits to losses in other areas. Managers should be cautioned, however, that values can be sensitive to many factors and that more theoretical and empirical research in this area is needed.

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NOTES

FOOD HABITS AND ALGAL ASSOCIATIONS OF JUVENILE LUMPFISH, *CYCLOPTERUS LUMPUS* L., IN INTERTIDAL WATERS

The lumpfish, *Cyclopterus lumpus* L., occurs in the north Atlantic Ocean, and is economically important in Maritime Canada (roe) and in Iceland, Greenland, and Europe (flesh and roe). Adults spawn in subtidal waters along rocky coasts and occasionally in intertidal waters (Benfey and Methven 1986). The spawning behavior and curious parental care by males was described in the 1800s and early 1900s (Yarrell 1841; Fulton 1907) and recently by Goulet et al. (1986). Juveniles, particularly age 0, have been encountered in pelagic waters (Blacker 1983; Daborn and Gregory 1983), in coastal areas (Bigelow and Schroeder 1953), and in intertidal waters (Proctor 1933; Moring 1985).

Examinations of the food habits of adult lumpfish have shown that the diet includes principally coelenterates, ctenophores, chaetognaths, various crustaceans, small fishes, and some molluscs and polychaetes (Cox and Anderson 1922; Bigelow and Schroeder 1953; Collins 1976; Gregory and Daborn 1982; Able and Irion 1985). Daborn and Gregory (1983), who examined the foods of juveniles in pelagic waters, found that surface-feeding amphipods and copepods were most important in the diet. With that exception, however, the foods consumed by juvenile lumpfish are largely unknown, particularly in intertidal areas.

The Cyclopteridae possess a ventral suction disc with which they adhere to rocks, lobster traps, or other firm objects. Juveniles are often encountered attached to marine algae as well, and in pelagic waters they have been encountered swimming freely and also attached to floating algae (Procter 1933; Forsman 1970; Daborn and Gregory 1983). In tidepools, however, juvenile lumpfish attach primarily to various species of marine algae—associations that have not been documented.

Juvenile lumpfish are seasonally present in Maine tidepools from June to December (Moring, unpubl. data). Occurrences after October are rare—as is typical for most intertidal fishes in Maine. In this study, I examine the foods of juvenile lumpfish during this seasonal period in intertidal areas and document their associations with algae in tidepools.

Materials and Methods

Juvenile lumpfish were collected primarily in three tidal pools: Blueberry, West Pond, and West Side, along Schoodic Peninsula, a portion of Acadia National Park near Winter Harbor, ME. Blueberry Pool, on the eastern side of the Peninsula, is in the middle to upper intertidal zone and is isolated at plus ebb tides <0.5 m. This pool was the deepest of the three (maximum depth averaged 53 cm during collecting trips). Total pool area, measured by compass and tape and computed on circumpolar paper, was 109 m^2 (95 m^2 of exposed pool surface: computed by subtracting area of exposed rocks from total pool area). Direct wave action is from the east, but the pool is effectively protected, being 20 m from open water. The anthophyte, *Zostera marina*, and 13 species of marine algae were identified in the pool during a species composition survey in July 1986.

West Pond Pool, along the southern edge of the Schoodic Peninsula, is the smallest of the three study pools, averaging 41 m^2 of total and exposed pool area. Maximum depth averaged 37 cm. A rock wall forms the eastern boundary of the pool in the lower intertidal zone. Direct wave action is from the southwest, and the pool is formed only during minus (<0.0 m) tides. Eleven species of marine algae were identified in the pool in July 1986, but *Z. marina* was not collected.

West Side Pool is the largest and shallowest of the pools. Total pool area averaged 106 m^2 (104 m^2 of exposed pool), and maximum depth averaged 36 cm during collecting trips. Direct wave action is from the west and pool isolation is less than two hours during ebb tides. *Zostera marina* and 14 species of marine algae were identified in the pool in July 1986.

Juvenile lumpfish were collected with long-handled dip nets during ebb tides and were measured (mm total length), and algal associations (attachments by ventral suction disc) were noted. These associations were noted by direct observation of fish on a species of algae prior to capture or by passing a net through a clump of algae of known species and dislodging fish. Based on unpublished data, samples represent 20–25% of total lumpfish juveniles in pools. Fish were preserved in 10% formalin and stomach contents of 150 fish were analyzed. Total

contents of stomachs and total number of each prey taxa were counted and weighed (mg wet weight). Food items were identified to major taxonomic groupings, and occasionally to genus or species. An Index of Relative Importance (Pinkas et al. 1971), which factors percentage frequency, weight, and numbers, was computed for each food item in stomachs.

Algal associations were observed during 43 sampling trips in the seasonal period of lumpfish presence in tidepools, 1979–86, principally in the three study pools. Trips ranged from a low of 2 in December to 10 in June and July during these years. Samples of fish for food analyses were collected from July to November (principally July and August) in 1981, 1984, and 1985. Food habits data were pooled because sample sizes were insufficient for monthly or yearly comparisons. Sampling trips averaged 80 minutes and were made exclusively during daylight ebb tides.

Results

Food

Amphipods were the principal item in the diet of 150 juvenile *C. lumpus* examined that ranged in length from 9 to 50 mm; peak length frequency was 15 mm. Copepods, isopods, cumaceans, and marine mites (Acarina) were also numerically important (Table 1). Two lumpfish had consumed larval fishes: one a smaller lumpfish and the other an unidentified species. Seven stomachs (4.7%) were empty. Amphipoda were also most important in weight. The Index of Relative Importance (IRI) indicates Amphipoda (IRI = 6,732) and Copepoda (IRI = 2,650) and, to a lesser extent, Isopoda (IRI = 798) were the most important items in the diet. Other foods were of only minor importance.

There was no significant difference in the diets of lumpfish between locations along Schoodic Peninsula (Table 1; $\chi^2 = 16.93$, $0.10 > P < 0.05$), except that Polychaeta were consumed in higher numbers at Blueberry Pool. More Cumacea and Copepoda were consumed by fish in West Side Pool, but this trend at West Side Pool may be a reflection of fish size and the presence of *Z. marina*—excellent microhabitat for Copepoda and Cumacea. These organisms were significantly more important in the diet of fish <15 mm ($\chi^2 = 32.0$; $P < 0.05$), while Amphipoda, Isopoda, and Polychaeta were more significant ($\chi^2 = 51.0$; $P < 0.01$) in the diet of juveniles ⩾15 mm TL than in the diet of smaller fish.

Algal Associations

Juvenile lumpfish observed were from 6 to 50 mm long and included primarily fish of age 0, but also age 1, as judged by length-frequency graphs and other work of Cox and Anderson (1922) and Daborn and Gregory (1983). One juvenile, 80 mm TL (apparently from an older year class), was also collected. From 328 observations of algal attachments of lumpfish during daylight hours, definite patterns emerged. *Zostera marina* and 18 species of marine algae were identified from the three pools during a survey in July 1986. Juvenile lumpfish were also found attached to an additional species, *Rhodymenia*

TABLE 1.—Percent occurrence and percent of total weight of food items in the diet of juvenile *Cyclopterus lumpus*, and foods by pool location and size (percent occurrence). West Pond data were not sufficient for inclusion in site comparisons, but are used in length comparisons; $n = 150$ for all three pools. Seven stomachs were empty (4.7%) and are not included in food data. Fish size range was 9–50 mm, with a length frequency peak of 15 mm.

Item	Occurrence %	Weight %	Pool		Total length of fish (mm)	
			Blueberry ($n = 78$)	West Side ($n = 62$)	<15 ($n = 60$)	⩾15 ($n = 83$)
Amphipoda	68	68	71	61	45	84
Copepoda	53	6	49	61	73	40
Isopoda	38	14	41	32	20	51
Cumacea	35	3	27	47	42	30
Acarina	20	1	18	23	20	19
Polychaeta	15	3	24	2	5	23
Mysidacea	3	1	3	5	3	4
Other items	[1]⩽3	4	—	—	—	—

[1]Other items, in order of decreasing percentage occurrence: Cladocera, fish eggs, Diptera, *Littorina* spp. (Gastropoda), *Mytilus edulis*, algae, fish larvae, Caprellidea, dinoflagellates, cypris larval stages, megalops larval stages.

palmata, in a different intertidal locale on the Maine coast. Fish were found attached to 12 of these species of algae, *Zostera marina*, and 1 invertebrate—the blue mussel, *Mytilus edulis*. Only two lumpfish were encountered free-swimming, without a substrate or algal association, during these daylight observations. In 39% of the observations, juveniles were primarily associated with one of three species of *Laminaria*. In areas without *Laminaria*, but with *Zostera marina*, however, fish were frequently associated with *Z. marina* (Table 2).

Associations with *Laminaria* were significantly higher ($\chi^2 = 251.4$; $P < 0.01$) than with *Z. marina* but, because algal species composition varies with locale, associations were also analyzed by location (Table 2). In West Side Pool, which contained almost no *Laminaria* spp., 76% of the associations were with *Zostera marina*. No one algal species was dominant in West Pond Pool. In Blueberry Pool, *Laminaria* is much more abundant (but <50% of algal surface area), and 67% of the associations were with that genus.

As juvenile lumpfish increase in size, fewer were associated with *Z. marina* and more with *Ascophyllum nodosum* (Table 2). The difference was significantly in favor of attachments to *Z. marina* for fish <19 mm, but significantly in favor of attachments to *A. nodosum* for lumpfish over 26 mm ($P < 0.05$, paired comparison *t* tests and chi-square tests). Areas containing *Z. marina* may thus be extremely important to juveniles <20 mm long, but the protective function of the plant decreases as fish size increases.

Discussion

Juvenile lumpfish in Maine appear to use intertidal areas seasonally during more than one year of life. An array of sizes of *C. lumpus* can be taken within a single tidepool (e.g., lengths of 9–49 mm from a single pool in August). Although most juveniles in intertidal areas were age 0, fish of age 1 were not rare, and one fish collected was probably age 2. An adult was also observed guarding a nest in a deep tidepool near Blueberry Pool in 1982.

The food of juveniles is less diverse than that of adults (as reported by others), probably because the younger fish have smaller mouths and less ability to capture prey. The availability of larger prey items may also be limited in tidepools; ctenophores and coelenterates are generally uncommon in such waters. However, the consumption of copepods and amphipods by more than half the juveniles examined in this study coincides well with the studies of Daborn and Gregory (1983) of juvenile lumpfish in surface waters offshore. Although it is commonly believed that adult lumpfish feed only during winter (Cox and Anderson 1922; Collins 1976), the juveniles assuredly feed in summer: <5% of the stomachs that I examined were empty.

The information presented here dealing with juvenile lumpfish and algae are field observations of in situ associations. Given a choice between several genera or species of algae, the algal preference might be different. However, data from Blueberry Pool, where *Z. marina* and at least 13 species of algae were present, showed that 67% of the juvenile lumpfish were encountered with *Laminaria* spp., even though those three species made up less than one half of the submerged algal surface area (visual estimation).

Because juvenile lumpfish are typically observed attached to marine algae or to *Z. marina*, the question remains why associations are with specific algae? There may be several possible explanations, including functional morphology of the fish species, coloration, hydraulics, and adhesion.

TABLE 2.—Algal and plant associations by *Cyclopterus lumpus* (%) by pool and total length.

Site or size (n)	Taxon					
	Laminaria spp. (3 species)	*Fucus vesiculosus*	*Ascophyllum nodosum*	*Agarum cribrosum*	*Zostera marina*	Others
Pool						
West Side (76)	0	13	5	0	76	6
West Pond (17)	29	29	24	0	2	16
Blueberry (150)	67	12	10	6	1	4
Total length (mm)						
≤12 (72)	34	13	4	5	33	11
13–18 (84)	47	11	8	4	27	3
19–24 (54)	43	15	11	6	20	5
≥25 (38)	49	13	18	0	8	12

Marine algae serve as arractants for invertebrates (Hicks 1986). Juvenile lumpfish are not rapid or efficient swimmers, and thus cannot effectively pursue active prey. It would seem advantageous for such fish to live in concentrations of algae near concentrations of invertebrates.

Second, unlike some species of tidepool fishes (e.g., *Oligocottus snyderi* and *Xererpes fucorum* of the Pacific coast), juvenile lumpfish show only limited variations in color. The brown-orange coloration of juveniles may explain why they prefer algal genera and species of similar coloration, such as *Laminaria*. This explanation does not hold for the large number of juveniles associating with *Z. marina*, which is green. However, the strong association with *Z. marina* apparently holds only for small lumpfish which feed heavily on small crustaceans (Tables 1, 2). Brown (1986) recently found that small juveniles (about 10 mm long) spent more time attached to structures than was spent swimming. Algae of any type or color may thus be especially important to the smallest fish, particularly if availability of brown algae is reduced in a particular locale (e.g., West Side Pool, where 60% of the fish were 15 mm, compared with 41% in Blueberry Pool). As lumpfish size increases, there appear to be increasing associations with brown algae and decreasing associations with green-colored *Z. marina*, even when both types are present (Table 2).

Third, *Laminaria* spp. can provide some protection for fish from direct wave action, perhaps more than from other genera or algal species present (for general concepts, see Wieser 1952, O'Connor et al. 1979, and Seed 1986). *Laminaria* often occurs in clusters, resulting in a diffusing of wave action that would otherwise displace fishes. The distribution of *L. saccharina* has been shown to be independent of exposure (Sze 1982). Lumpfish associated with this functional type of alga may be effectively protected at flood tides from full wave action, and at ebb tides from avian or terrestrial predators.

Finally, the ability of lumpfish to attach to objects has been well documented; juveniles of the sizes collected in the tidepools of Schoodic Peninsula, ME can adhere to objects and withstand water speeds of up to 170 cm/s (Gibson 1969). Lumpfish use this attachment ability to avoid the adverse impacts of wave action (Alexander 1967). Suction efficiency would be improved by adherence to a flat, somewhat rigid surface. though several species of marine algae have smooth, nonrippled fronds, species of *Laminaria* provide the most surface area of this type in the pools examined.

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GENETIC POPULATION STRUCTURE OF CHINOOK SALMON, *ONCORHYNCHUS TSHAWYTSCHA*, IN THE PACIFIC NORTHWEST

F. UTTER,[1] G. MILNER,[1] G. STÅHL,[2] AND D. TEEL[1]

ABSTRACT

Variation at 25 polymorphic protein coding loci was examined for 86 populations of chinook salmon, *Oncorhynchus tshawytscha*, ranging from the Babine River in British Columbia to the Sacramento River in California. Substantial differences in allele frequencies identified patterns of genetic variability over the geographic range of the study. The following nine major genetically defined regions were formulated: 1) the Fraser River tributaries east of the Cascade Crest (no downstream drainages were sampled), 2) Georgia Strait, 3) Puget Sound, 4) a broad coastal region ranging from the west coast of Vancouver Island southward through northern California, 5) the Columbia River below The Dalles Dam, 6) the Columbia River above The Dalles Dam, 7) the Snake River, 8) the Klamath River, and 9) the Sacramento River. Populations sampled within a region tended to be genetically distinct from each other although they exhibited the general patterns of variability that defined the region. Within a region there was little distinction among populations returning to spawn at different times. The persistence of these geographic patterns in the face of natural opportunities for introgression, and sometimes massive transplantations, suggests that genetically adapted groups within regions have resisted large-scale introgression from other regions. Repopulation of deglaciated areas in the Fraser River, Georgia Strait, and Puget Sound apparently occurred from multiple sources; most likely sources included Columbia River populations and northern refuges rather than from the large coastal group of populations. Patterns of genetic distribution of chinook salmon differed from those of other anadromous salmonids studied within this region. A conservative policy for stock transfers was suggested based on distinct genetic differences observed both between and within regions.

Population studies of chinook salmon, *Oncorhynchus tshawytscha*, based on electrophoretically detected genetic variation have been carried out since the late 1960s. As data have accumulated, an increasingly clear picture of the breeding structure of this species has emerged. While early investigations based on only a few polymorphic loci identified differences among populations, they failed to identify any geographic trends (e.g., Utter et al. 1973; Kristiansson and McIntyre 1976). Differences within and among drainages became apparent as additional polymorphic loci were found and a more comprehensive sampling of populations was made (Utter et al. 1976, 1980; Gharrett et al. 1987).

This paper outlines the genetic structure of chinook salmon in the Pacific Northwest using allele frequency data collected for the purpose of estimating the stock composition of ocean caught chinook salmon (Milner et al. 1981[3]; 1983[4]; Miller et al. 1983; Utter et al. 1987). Our purpose is to examine these data in the light of other relevant biological and historical information 1) to understand genetic relationships among chinook salmon populations better and 2) to provide biologists with new insights to assist in the preservation and management of this important biological resource.

MATERIALS AND METHODS

Our data were obtained from samples of juvenile or adult fish collected at 86 locations ranging from British Columbia through California (Table 1, Fig. 1). These data include allele frequencies from 25 protein-coding loci with sample sizes between 38 and 200 individuals. Data were accumulated between 1980 and 1984 and were reported in part in Milner et al. (fn. 3, 4).

Electrophoretic procedures followed those de-

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[3]Milner, G. B., D. J. Teel, F. M. Utter, and C. L. Burley. 1981. Columbia River stock identification study: Validation of genetic method. Report to Bonneville Power Administration under contract DE-A179-80BP18488, 51 p. Available Bonneville Power Administration, P.O. Box 3621, Portland, OR 97208.

[4]Milner, G. B., D. J. Teel, and F. M. Utter. 1983. Genetic stock identification study. Report to Bonneville Power Administration under contract DE-A179-82BP28044M001, 95 p. Available Bonneville Power Administration, P.O. Box 3621, Portland, OR 97208.

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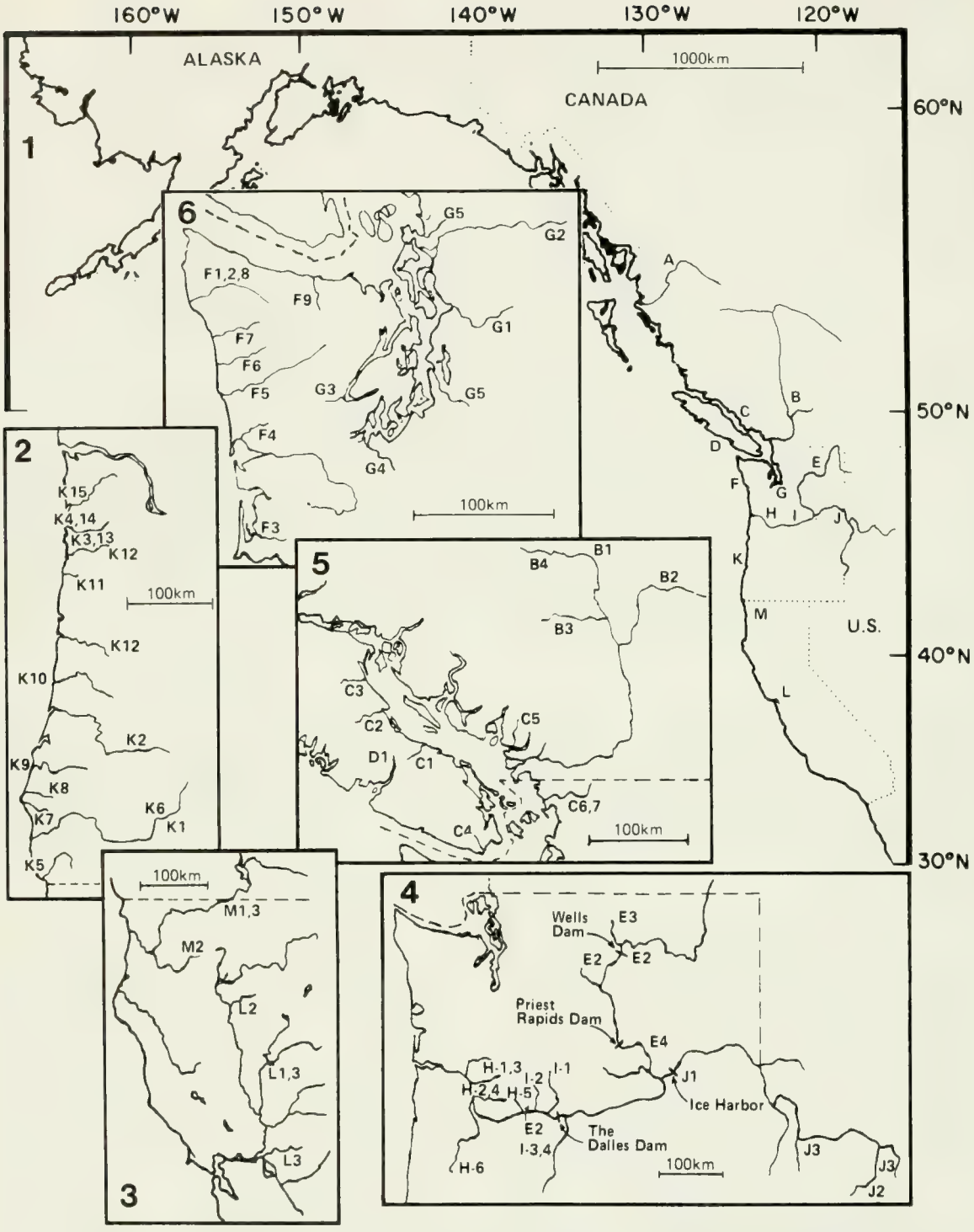

FIGURE 1.—Locations of sample collections based on map code of Table 1. 1. Total range of sampling identifying general locations or drainage systems. 2. Oregon (OR) coast. 3. California (CA). 4. Columbia River. 5. Georgia Strait, British Columbia (BC) coast, and Fraser River. 6. Washington (WA) coast and Puget Sound.

TABLE 1.—Chinook salmon collections made from British Columbia through California. Map codes refer to Figure 1. Samples representing a hatchery stock are marked by $. Locations followed by (a) represent adult samples; all other samples were from juvenile fish. Season of return identifies the time of entry by adults into freshwater. Pooled samples are indicated by hyphens.

Map code	Location of samples	Area or drainage system	Region	Sample size	Season of return
A1	Babine (a)	Skeena R.	Inland	39	Summer
B1	Tete Jaune (a)	Fraser R.	Inland	38	Summer
B2	Clearwater (a)	Fraser R.	Inland	45	Summer
B3	Chilco	Fraser R.	Inland	49	Summer
B4	Stuart–Nechako (a)	Fraser R.	Inland	105	Summer
C1	$Big Qualicum	Georgia Strait	Coastal	85	Fall
C2	$Puntledge (a)	Georgia Strait	Coastal	100	Fall
C3	$Quinsam (a)	Georgia Strait	Coastal	97	Fall
C4	$San Juan	Georgia Strait	Coastal	50	Fall
C5	$Capilano	Georgia Strait	Coastal	99	Fall
C6	Nooksack, south fork	Georgia Strait	Coastal	50	Spring
C7	Nooksack, north fork	Georgia Strait	Coastal	50	Spring
D1	$Robertson Ck. (a)	British Columbia coast	Coastal	100	Fall
E1	$Wells Dam	Upper Columbia R.	Inland	50	Summer
E2	$Carson–$Leavenworth[1]	Upper Columbia R.	Inland	148	Spring
E3	$Winthrop	Upper Columbia R.	Inland	129	Spring
E4	$Priest Rapids	Upper Columbia R.	Inland	100	Fall
F1	$Soleduck	Washington coast	Coastal	100	Summer
F2	$Soleduck	Washington coast	Coastal	100	Spring
F3	$Naselle	Washington coast	Coastal	99	Fall
F4	$Humptulips	Washington coast	Coastal	50	Fall
F5	$Quinault	Washington coast	Coastal	100	Fall
F6	Queets	Washington coast	Coastal	120	Fall
F7	Hoh	Washington coast	Coastal	100	Fall
F8	$Soleduck	Washington coast	Coastal	50	Fall
F9	$Elwha	Washington coast	Coastal	100	Fall
G1	$Skykomish	Puget Sound	Coastal	100	Summer
G2	$Skagit	Puget Sound	Coastal	100	Summer
G3	$Hood Canal	Puget Sound	Coastal	98	Fall
G4	$Deschutes	Puget Sound	Coastal	150	Fall
G5	$Green R.–$Sammish	Puget Sound	Coastal	149	Fall
H1	$Cowlitz–$Kalama	Lower Columbia R.	Coastal	100	Spring
H2	$Lewis R.	Lower Columbia R.	Coastal	50	Spring
H3	$Cowlitz (a)–$Kalama	Lower Columbia R.	Coastal	149	Fall
H4	$Lewis R.	Lower Columbia R.	Coastal	50	Fall
H5	$Washougal R.	Lower Columbia R.	Coastal	50	Fall
H6	$Eagle Ck.–$McKenzie R.	Lower Columbia R. (Willamette)	Coastal	88	Spring
I1	$Klickitat R.	Mid-Columbia R.	Inland	50	Spring
I2	$Spring Ck.–$Big Ck.[2]	Mid-Columbia R.	Inland	150	Fall
I3	$Warm Springs–$Round Butte (a)	Mid-Columbia R.	Inland	109	Spring
I4	Deschutes (a)	Mid-Columbia R.	Inland	49	Fall
J1	Ice Harbor (a)	Snake R.	Inland	200	Fall
J2	McCall–Johnson Ck.	Snake R.	Inland	106	Summer
J3	$Rapid R.–Valley Ck.[3]	Snake R.	Inland	165	Spring
K1	$Cole R.–Hoot Owl Ck.	Oregon coast	Coastal	163	Spring
K2	$Rock Ck.	Oregon coast	Coastal	100	Spring
K3	$Cedar Ck.	Oregon coast	Coastal	99	Spring
K4	$Trask R.	Oregon coast	Coastal	100	Spring
K5	Chetco	Oregon coast	Coastal	100	Fall
K6	Lobster Ck.	Oregon coast	Coastal	50	Fall
K7	$Elk R.	Oregon coast	Coastal	100	Fall
K8	Sixes R. estuary	Oregon coast	Coastal	100	Fall
K9	Coquille R. estuary	Oregon coast	Coastal	115	Fall
K10	Siuslaw Bay	Oregon coast	Coastal	82	Fall
K11	$Salmon R.	Oregon coast	Coastal	99	Fall
K12	$Nestucca R.–$Alsea R.[4]	Oregon coast	Coastal	346	Fall
K13	$Cedar Ck.	Oregon coast	Coastal	100	Fall
K14	$Trask R.–Tillamook Bay	Oregon coast	Coastal	188	Fall
K15	Nehalem estuary	Oregon coast	Coastal	141	Fall

[1]Includes Little White Salmon.
[2]Includes Little White Salmon.
[3]Includes Sawtooth and Red River.
[4]Includes Siletz Estuary and $Fall Creek.

TABLE 1.—*Continued.*

Map code	Location of samples	Area or drainage system	Region	Sample size	Season of return
L1	$Feather R.	Sacramento R.	Coastal	50	Spring
L2	$Coleman–$Nimbus	Sacramento R.	Coastal	300	Fall
L3	$Feather R.–$Mokelumne	Sacramento R.	Coastal	200	Fall
M1	$Trinity R.	Klamath R.	Inland	50	Spring
M2	$Iron Gate	Klamath R.	Inland	99	Fall
M3	$Trinity R.	Klamath R.	Inland	100	Fall

scribed in Aebersold et al. (1987). Buffer systems included the following: 1) a Tris-boric acid, EDTA system (pH 8.5) (Boyer et al. 1963); 2) an amine (3-aminopropyl morpholine) citrate system (pH 6.5) (Clayton and Tretiak 1972); and 3) a discontinuous Tris-citric acid (gel pH 8.15), lithium hydroxide, boric acid (electrode pH 8.0) system (Ridgway et al. 1970). Methods for visualizing enzyme activity followed Siciliano and Shaw (1976) and Harris and Hopkinson (1976). A system of nomenclature suggested by Allendorf and Utter (1979) was used to designate loci and alleles.

The 25 polymorphic loci (Table 2) were selected from a larger set of loci known to be variable in chinook salmon. Variable loci were excluded when data were unavailable for one or more of the sampling locations listed in Table 1. Much of the descriptive data for the loci and alleles were previously reported (Utter et al. 1980; Milner et al. fn. 4). Two previously unreported polymorphic enzymes in chinook salmon, Gr and Gpi-1(H), were used for population studies and are described in the appendix.

Allele frequencies were calculated directly from phenotypic classes for 14 nonduplicated loci. Tests for departures of genotypes from the expected binomial distribution (Hardy-Weinberg equilibrium) were made using a G statistic (Sokal and Rohlf 1969) with degrees of freedom equaling the number of expected genotypes minus the number of alleles. The isoloci Aat-1,2; Idh-3,4; Mdh-1,2; Mdh-3,4; and Pgm-1,2 (see Allendorf and Thorgaard 1984) were excluded from such tests because every individual was scored on the basis of four allelic doses from two loci. Combined allele frequencies of both loci were calculated directly from phenotypic expressions and were assumed to be the same at both loci for statistical calculations. The data for the Gpi-2 locus and the *Gpi-1(H)* allele were also excluded from Hardy-Weinberg calculations because common homozygotes and heterozygotes could not be reliably distinguished, and allele frequency estimates were

TABLE 2.—Background information on chinook salmon tissue samples for protein coding loci.

Protein name and enzyme number	Locus	Tissue[1]	Buffer system	Reference[2]
Aconitate hydratase (4.2.1.3)	Ah	L	2	1
Adenosine deaminase (3.5.4.4)	Ada-1	E,H,M	1	1
Aspartate aminotransferase (2.6.1.1)	Aat-1,2	H,M	1	1
	Aat-3	E	1	1
Dipeptidase (3.4.13.11)	Dpep-1	E,H,M	1,3	1
	Dpep-2	E	1,3	1
Glucose-6-phosphate isomerase (5.3.1.9)	Gpi-1	M	3	2
	Gpi-2	M	3	1
	Gpi-3	M	3	1
Glutathione reductase (16.4.2)	Gr	E,M	1,3	2
Isocitrate dehydrogenase (1.1.1.42)	Idh-3,4	E,L,H,M	2	1
Lactate dehydrogenase (1.1.1.27)	Ldh-4	E,L,M	1	1
	Ldh-5	E	1	1
Malate dehydrogenase (1.1.1.37)	Mdh-1,2	L,H,M	2	1
	Mdh-3,4	E,H,M	2	1
Mannose-6-phosphate isomerase (5.3.1.8)	Mpi	E,L.H.M	1	1
Phosphoglucomutase (2.7.5.1)	Pgm-1,2	E,L,H,M	2	1
Phosphoglycerate kinase (2.7.2.3)	Pgk-2	E,L,M	2	1
Superoxide dismutase (1.15.1.1)	Sod	L	1	1
Tripeptide aminopeptidase (3.4.11.4)	Tapep-1	E,H,M	3	1

[1]L = liver, E = eye, H = heart, M = muscle.
[2]1 = Milner et al. 1983, 2 = variation described in this study

based on the frequency of homozygotes for the respective variant alleles. Expected heterozygosities were calculated for polymorphic loci. Pairwise comparisons were made for all loci between all populations by a contingency table analysis using a G statistic. Two or more sample collections lacking significant allele frequency differences for any polymorphic locus were considered a single population. All subsequent analyses were performed on the resulting 65 individual and pooled populations. A critical value of 1% was used (for both the Hardy-Weinberg and the pairwise population comparisons) to reduce the erroneous rejection of the null hypothesis when using multiple tests. Nei's (1975) measure of genetic distance (D) was used to compare pairwise levels of genetic divergence between individual or pooled populations. A dendrogram based on a matrix of these comparisons was constructed by the unweighted pair group method (UPGM) (Sneath and Sokal 1973). Principal component analysis of the allele frequency data followed procedures outlined in Sneath and Sokal (1973). A nested gene diversity analysis followed procedures described by Nei (1973) and Chakraborty (1980) and was performed through the NEGST computer program described by Chakraborty et al. (1982).

RESULTS AND DISCUSSION

Tests for Hardy-Weinberg Equilibrium

Tests for significant deviations from Hardy-Weinberg proportions were made on each of the 86 data sets for 14 loci including Ah, Ada-1, Aat-3, Dpep-1, Dpep-2, Gpi-1 (excluding the subsequently described *Gpi-1(H)* allele affecting heterodimer formation), Gpi-3, Gr, Ldh-4, Ldh-5, Mpi, Pgk-2, Sod-1, and Tapep-1. Six deviations were observed (Table 3). These deviations probably were random errors expected from the 1,204 independent calculations at the 1% level of significance. The direction of the deviations indicates both excesses and deficits of heterozygotes in both instances where the same locus is involved (Mpi and Sod-1). Two of the populations having significant deviations, Eagle Creek and Stuart, were combined for subsequent analysis with other populations having Hardy-Weinberg proportions; combinations were based on overall nonsignificant differences of allele frequencies. The high significance of the Stuart sample for Sod-1 is inflated through an expected value less than unity for the homozygous genotype of the (*−260*) allele.

TABLE 3.—Populations and loci with significant (α = 0.01) departures from expected Hardy-Weinberg proportions.

Population (map code)	Locus	Level of significance	Excess*/deficit- of heterozygotes
Queets (F6)	Dpep-1	0.005	+
Humptulips (F4)	Mpi	0.01	−
Washougal (H5)	Mpi	0.005	+
Lobster Creek (K6)	Pgk-2	0.005	+
Eagle Creek (H6)	Sod-1	0.005	+
Stuart (B4)	Sod-1	0.0001	−

Description of Allelic Distribution

The allele frequencies observed for all 25 polymorphic loci over the geographic range of this study (Appendix) indicate considerable heterogeneity among loci with regard to levels of variation and geographic distribution. This variation is summarized from three perspectives—heterozygosity, frequency range for common allele, and index of gene diversity (G_{st}) (Table 4). Heterozygosity measures within-population variation. Those loci having higher heterozygosities have greater potential for divergence of allele frequencies among populations. Mean heterozygosity over all loci was 0.102, and five loci (Ah, Mpi, Pgk-2, Sod-1, Tapep-1) exceeded 0.200.

The range of allele frequencies and the index of gene diversity reflect the actual divergences observed among populations. The range is a simple identification of allele frequency extremes. The index of gene diversity is a quantitative measure of genotype deviations of the overall data set from those expected in a single panmictic population. Seven of the eight most heterozygous loci (Pgk-2, Mpi, Sod-1, Ah, Tapep-1, Gpi-2, Dpep-1) were among the eight loci having either the greatest range in frequency or the highest index of gene diversity, indicating considerable genetic differences among the populations samples. Typically, adjacent populations tended to have allele frequencies more similar to one another than to those from other areas (see Appendix). Notable examples include the following: 1) restriction of Gpi-2 variation largely to coastal populations from Vancouver Island through Oregon, 2) the highest frequency of the *Gpi-1(H)* allele in populations from the Sacramento River, 3) Aat-3 variation that is largely restricted to populations from Georgia Strait and western Vancouver Island, 4) low frequencies of variant alleles for most loci in all Klamath River populations and in spring and summer run populations from the Snake River, and 5) high frequencies of Tapep-1 variants in Puget Sound populations.

Two procedures for graphic analysis (a dendrogram [Fig. 2] based on pairwise genetic distance

TABLE 4.—Outline of frequency range for common alleles, heterozygosity, and diversity for 25 polymorphic loci of chinook salmon sampled from British Columbia through California. Single entries for isoloci assume identical allele frequencies for individual loci. Locations and areas are based on map codes of Table 1 and Figure 1. Only areas are identified when one or more populations of an area have a maximum value of 1.000. Both locations and areas are identified for maximum values less than 1.000.

Locus	Frequency range for common allele (location and area)		Heterozygosity	Diversity (Gst)
	Minimum	Maximum		
Ah	0.366 (C3)	1.000 (I,J,M)	0.232	0.091
Ada-1	0.865 (G1)	1.000 (C–F,H,I,K–M)	0.044	0.045
Aat-1,2	0.888 (G3)	1.000 (A–C,E,F,H–J,L,M)	0.030	0.035
Aat-3	0.735 (C2)	1.000 (B,E–M)	0.030	0.143
Dpep-1	0.652 (K3,K9)	1.000 (B,D,E,J,M)	0.164	0.116
Dpep-2	0.939 (B3)	1.000 (A–M)	0.004	0.045
Gpi-1	0.576 (L1)	1.000 (A–K,M)	0.040	0.245
Gpi-2	0.432 (K5)	1.000 (A–C,E–I,K–M)	0.169	0.310
Gpi-3	0.875 (B3)	1.000 (C,E–M)	0.022	0.060
Gr	0.420 (H6)	1.000 (C,D,F,G,I,K–M)	0.068	0.215
Idh-3,4	0.862 (E2)	1.000 (B,C,K,M)	0.080	0.040
Ldh-4	0.933 (B2)	1.000 (A–M)	0.009	0.037
Ldh-5	0.964 (E4)	1.000 (A–M)	0.008	0.017
Mdh-1,2	0.945 (K8)	1.000 (A–M)	0.003	0.023
Mdh-3,4	0.843 (C3)	1.000 (A–C,H,K,M)	0.040	0.025
Mpi	0.386 (H4)	0.990 (M3)	0.401	0.089
Pgm-1,2	0.903 (K3)	1.000 (A–M)	0.031	0.041
Pgk-2	0.062 (J2)	0.931 (H6)	0.420	0.153
Sod-1	0.530 (I2)	0.990 (M2)	0.345	0.086
Tapep-1	0.483 (G5)	1.000 (B,M)	0.226	0.134
Average	0.724	0.996	0.102	0.123

measures, and plots of principal component scores) assist in identifying patterns of allelic variability. The approximate location of each population is identified in Figure 2 on the basis of its inclusion in one of eight clusters (diverging beyond a genetic distance of 0.01) or major subgroupings (below a genetic distance of 0.01). A notable feature of Figure 2 is the geographic basis for much of the aggregation. For instance, clusters 1 and 2 represent downstream populations of the Columbia River, cluster 3 contains the two northernmost populations of Georgia Strait, and cluster 4 is comprised of coastal populations from Vancouver Island southward through Oregon. The nine population units shown in Figure 2 are explained in the following section and represent a synthesis of possible relationships among these 65 populations.

The two plots of principal components (Fig. 3) provide an alternative picture of the allelic variation based on different perspectives of the total variance in a multidimensional space. The first four principal components (PC), which account for almost 80% of the total genetic variation, also project a geographic picture of this variation in these plottings. Six of nine population groupings (described in the next section) are essentially resolved by PC1 and PC2. Two of the remaining units are resolved by PC3 and PC4.

We used three different hierarchies in the gene diversity analysis to give a more detailed examination beyond the data on gene diversity presented in Table 4 (Table 5). The hierarchies based on geographic and temporal clusters are discussed at this point; the hierarchy based on population unit clusters is discussed following the synthesis of these units. The geographic hierarchy was based on the locations of the samples using two regions (inland and coastal) with six areas within the inland region and seven areas within the coastal region (see Table 1).

The within-population component of gene diversity (i.e., the mean average heterozygosity) in each hierarchy was 87.7% of the total diversity (i.e., the expected heterozygosity based on the mean allele frequencies). The remaining 12.3% of the total diversity was the index of gene diversity, G(st) resulting from population subdivision (see also Table 5). Most of the gene diversity in the geographic hierarchy was due to genetic differences between populations within areas (4.6%) and areas within regions (6.2%). The regional component contrasting inland populations of major drainages with populations from downstream tributaries and coastal drainages contributed only 1.5% of the total diversity. By far the largest portion of subdivision in the temporal

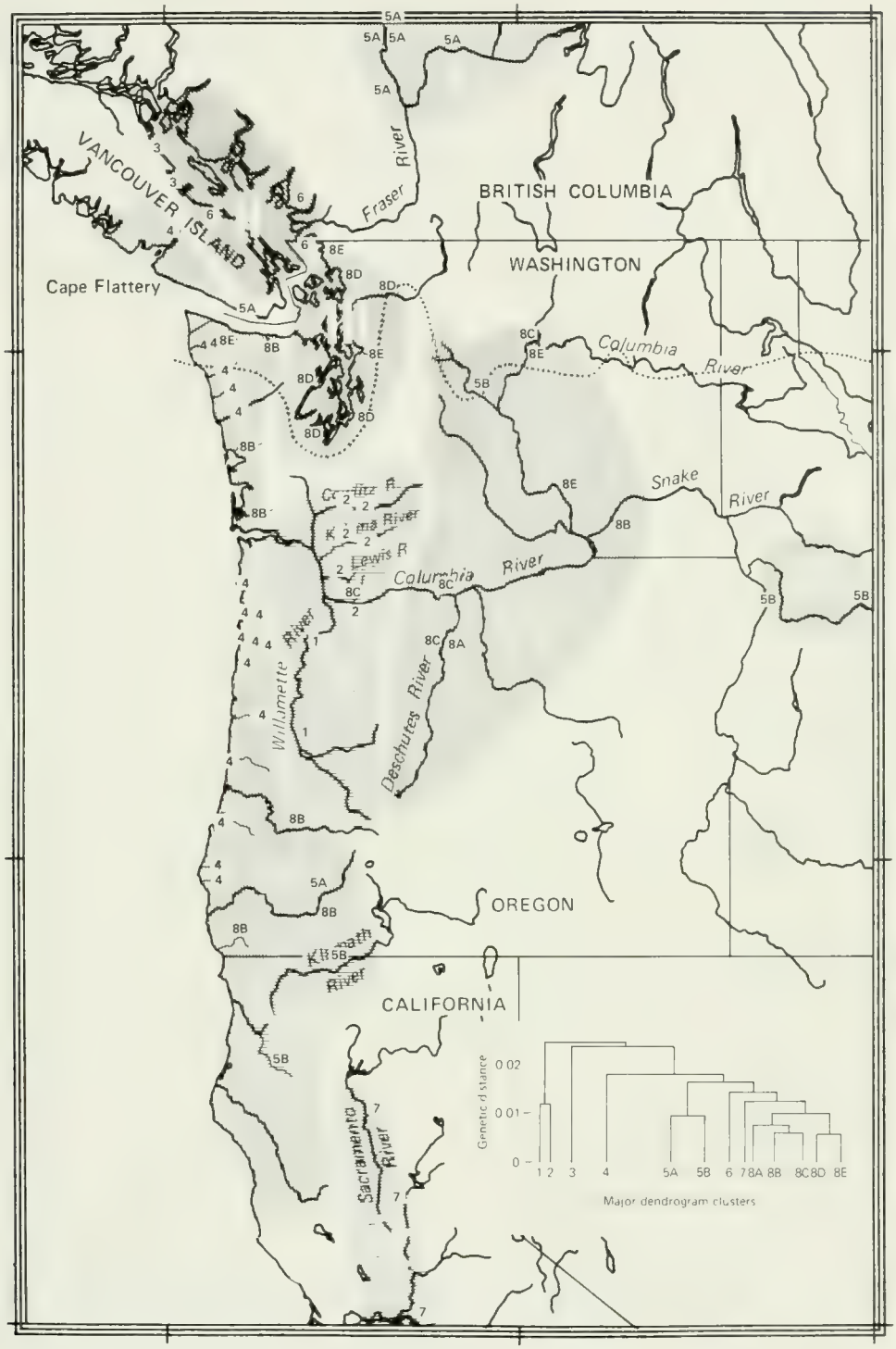

FIGURE 2.—Dendrogram and nine population units formulated from allele frequency data of this study. Populations are approximately located by numbered squares which identify membership in clusters on the superimposed genetic distance dendrogram. An exception is the most northern location of Unit I (Babine River) which lies beyond map range. Dotted line represents maximum glaciation during late Pleistocene (McPhail and Lindsey 1986).

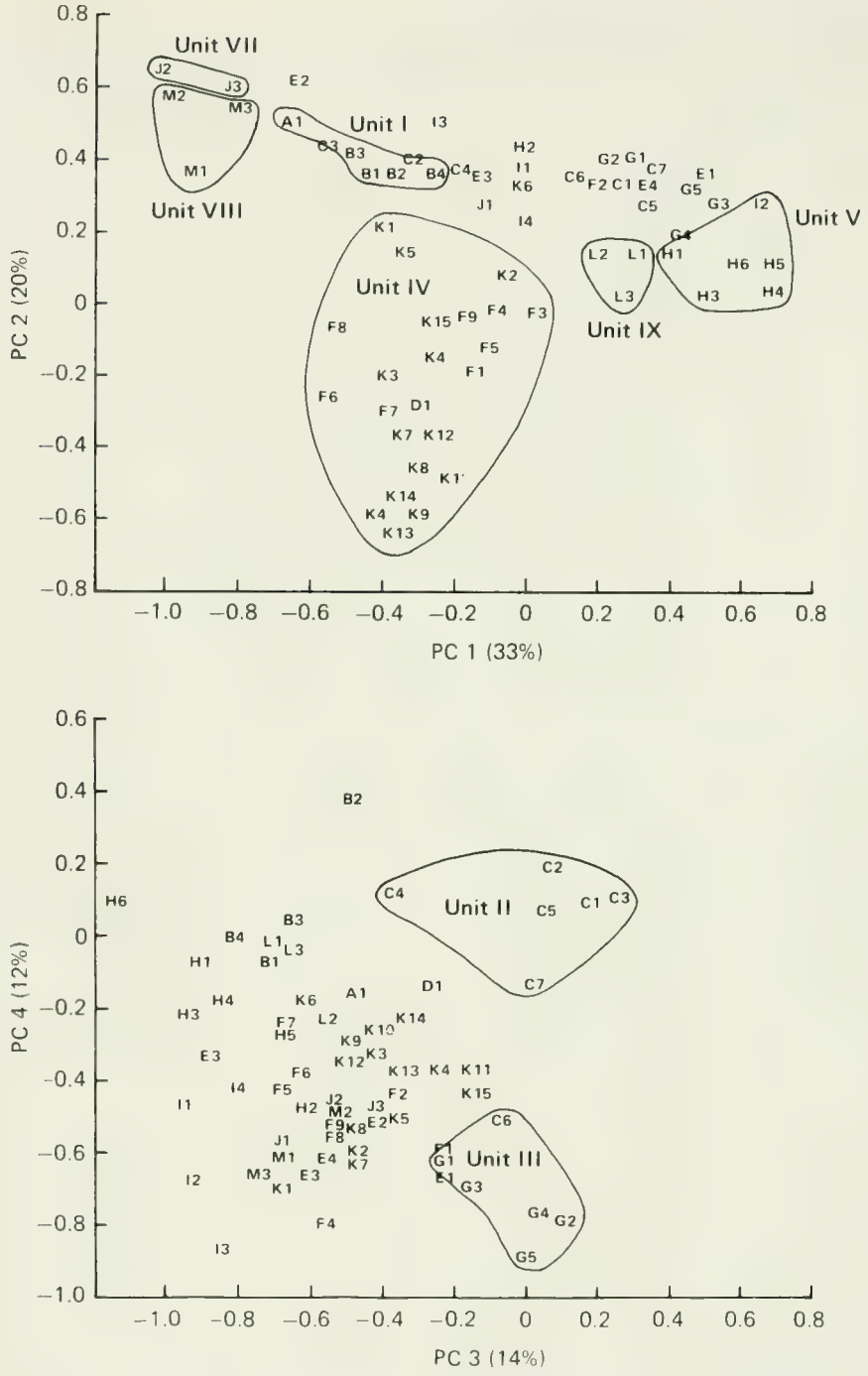

FIGURE 3.—Plots of scores for principal components 1 & 2 and 3 & 4 derived from allele frequencies in the Appendix. Major contributing loci include PC1 - Mpi, Pgk-2, Sod, and Tapep-1; PC2 - Ah, Dpep-1, Gpi-2, and Pgm-1,2; PC3 - Aat-3, Gr, and Tapep-1; PC4 - Mpi.

TABLE 5.—Summary of distribution of relative gene diversity of chinook salmon in geographical and temporal hierarchies based on 65 individual or pooled populations and 25 polymorphic loci. Areas, regions, and seasons are given for each population in Table 1. Absolute values of gene diversity include mean average heterozygosity (Hs) - 0.1018 and total diversity (Ht) - 0.1161.

Geographic clusters	%	Temporal clusters	%	Population unit clusters	%
Within populations	87.7	Within populations	87.7	Within populations	87.7
Between populations, within areas	4.6	Between populations, within seasons	11.4	Between populations, within units	4.4
Between areas, within regions	6.2	Between seasons	0.9	Between units	7.9
Between regions	1.5				
Total	100.0		100.0		100.0

hierarchy resulted from differences between populations within seasons (11.6%), with only 0.7% of the total diversity being due to differences between seasons.

Interpretation of Observed Variation

We interpreted the overall data set primarily as a reflection of patterns and levels of gene exchange among populations. This interpretation does not exclude the possibility of some selective forces influencing the frequencies of some alleles and genotypes in some environments (e.g., Powers et al. 1983; Mork et al. 1984). However, empirical data from diverse animal species justify an assumption of predominant neutrality (Ihssen et al. 1981; Chakraborty et al. 1980; Eanes 1987). This assumption is strengthened when many polymorphic loci are examined and is particularly pertinent in anadromous salmonids where restricted population sizes accentuate the influence of genetic drift (Utter et al. 1980). The data presented here indicate that chinook salmon consist of a genetically complex network of populations throughout the geographic range of this study. This information yields some clear conclusions and suggests a number of additional possibilities that must await confirmation or rejection from additional studies.

One conclusion is that the time of return (i.e., season) is not a major factor in establishing relationships of stocks among areas. Both the geographic clustering in Figures 2 and 3 and the small between-seasons component of the temporal gene diversity analysis point away from the concept of a recent common ancestry of fish returning at the same time in different areas. This finding comes as no surprise based on published data of other anadromous salmonids (e.g., rainbow trout, Allendorf and Utter 1979). However, it is still commonly accepted that the chinook salmon is separated into temporally distinct "races" (e.g., McClane 1978). Although a strong genetic component for the time of return has been clearly demonstrated in anadromous salmonids (e.g., Helle 1981), and this is not debated here, it appears that genetic divergence into temporally distinct units tends to occur within an area from a common ancestral stock of chinook salmon.

In contrast to the lack of evidence for genetic structuring of time of return, a geographic basis for genetic structuring is apparent. The relatively large area component of gene diversity (over half of the between-population diversity in column 1 of Table 5) coupled with the predominantly geographic clusterings warrant an attempt to define different geographically discrete population units. Most units (Figure 2 and Appendix) incorporate one or more of the areas or drainage systems listed in Table 1. Inevitably, overlap occurs between these formulated population units and the a priori groupings of areas or drainages.

The Fraser River grouping (unit I) is necessarily limited to the upstream areas because no downstream populations were sampled. The single sample from the Babine River, tributary to the Skeena River and adjacent to drainages of the upper Fraser River, is also tentatively included in Unit I. The Babine population aggregates with those of the Fraser River in the dendrogram (cluster 5A) and the plots of PC1 and PC2. Most populations of Unit I (including the Babine) are distinguished by the presence of the *Gr-110* allele at a mean frequency of 0.05. This allele was not included in the Appendix or in most analyses because of the incomplete data sets from some coastal populations. The *Gr-(110)* allele was not observed in other populations that aggregate in the dendrogram and PC plots with those of unit I; these populations include the San Juan River (southern Vancouver Island), the spring- and summer-run fish of the Snake River, and the Klamath River.

The population unit of Georgia Strait (unit II) comprises populations forming clusters 3 and 6 in the dendrogram, plus the San Juan River population. These six populations aggregate adjacently in the plottings of PC3 and PC4. Populations of Unit II typically have relatively high allele frequencies of *Aat-3 (90)*, *Pkg-2 (90)*, and *Tapep-1 (130)*, although exceptions occur at each locus. Carl and Healey (1984) reported similar high frequencies for allelic variations of Aat-3 and Tapep in a study of chinook salmon populations of the Nanaimo River which flows from Vancouver Island into Georgia Strait.

Populations in the Puget Sound unit (Unit III), bounded to the north by the population from the South Fork of the Nooksack River, aggregate fairly clearly in both the dendrogram (clusters 8D and 8E) and the plots of PC3 and PC4. The cohesiveness among the fall-run populations vary likely reflects both genetic isolation and present (or very recent) gene flow through transfers among hatcheries. Like unit II, populations of unit III also have high allele frequencies for *Tapep-1 130*; in fact, it has the highest mean frequencies for this allele among the nine population units that were formulated. However, the mean frequencies of the common (i.e., 100) alleles for Aat-3 and Pgk-2 are much higher in unit III than in unit II. No influence of reported transfers of lower Columbia River fish to Puget Sound hatcheries (e.g., Ricker 1972) is apparent from the graphic projections or the allelic data.

An extended grouping of coastal populations (unit IV) ranges from northern California (see Utter et al. 1980) to Robertson Creek on the west coast of Vancouver Island. Populations of the Columbia, Klamath, and Sacramento Rivers are excluded from unit IV. This unit is distinguished by high frequencies of the *Gpi-2 (60)* allele and (in most instances) some Pgm variation. Most populations appear either in clusters 4 or 8B of the dendrogram and aggregate distinctly in the plottings of PC1 and PC2. Two populations are retained in Unit IV for geographic consistency which do not congregate with other populations of this unit; the spring run returning to the Soleduck River on the Washington coast, and the Lobster Creek population returning to the upper Rogue River on the Oregon coast. The outlying of the Soleduck spring-run population appears to be related to its heterogeneous origins. Records indicate that this run originated from crosses of fish from the Cowlitz River (lower Columbia River) and Umpqua River (Oregon coast) with some contribution from the spring run of the Dungeness River, a drainage entering the Strait of Juan de Fuca (C. Johnson[5]). An explanation for the outlying of the Lobster Creek population is less apparent and requires further investigation.

Two individual and four paired hatchery populations sampled from the lower Columbia River form a geographically and genetically discrete unit (unit V). This group represents the most divergent pair of clusters (1 and 2) on the dendrogram and generally aggregates distinctly in the plotting of PC1 and PC2. Populations of unit V are particularly distinguished by high allele frequencies of *Gr (85)* and *Mpi (109)*. Unit V is bounded upstream by the U.S. Fish and Wildlife Service Spring Creek Hatchery population (Spring Creek Hatchery is located on the pool impounded by Bonneville Dam). The pairing of four of the six populations is consistent with high levels of gene flow resulting from an extensive history of transplantation among the populations of the lower Columbia River (Simon 1972; Howell et al. 1985). This group's distinctness from other groups is also consistent with a minimal impact of transplantations of these populations beyond the lower Columbia River on indigenous populations in other areas (e.g., Cowlitz spring-run fish to the Snake River, C. Burley[6]; Kalama fall-run fish to Puget Sound, mentioned above).

The upper Columbia River unit (unit VI)—more than any of the other groupings—is composed of genetically diverse elements placed together more on the basis of geographic convenience rather than genetic unity. Unit VI is somewhat loosely bounded downstream by populations of the Klickitat and Deschutes Rivers; both rivers enter the Columbia River near The Dalles Dam. Unit VI's component populations include individuals of mixed ancestral origins, along with others of presumably pure lineage. Two populations known to have mixed ancestral origin are those of the U.S. Fish and Wildlife Service Carson and Leavenworth Hatcheries. The Carson Hatchery population (located on the Wind River which drains into the Bonneville pool) was derived from interceptions of spring-run fish destined for areas of the upper Columbia and Snake Rivers. The Leavenworth population (combined with Carson in the analyses) has been largely maintained by continued infusions from fish of the Carson Hatchery (Howell et al. fn. 5). The Ice Harbor population—another group of mixed ancestral origins—is composed of fall-run fish destined for different areas within the Snake River that were intercepted at Ice Harbor Dam near the mouth of the Snake

[5]C. Johnson, Washington Department of Fisheries, General Administration Bldg., Olympia, WA 98504, pers. commun. May 1985.
[6]C. Burley, U.S. Fish and Wildlife Service, 9317 Highway 99, Vancouver, WA 98665, pers. commun. May 1985.

River. This population is included in unit VI because of its geographic proximity and genetic similarity to populations of unit VI contrasted with its distinctness from spring- and summer-run populations of the upper Snake River.

Populations of purer lineage within unit VI aggregate within cluster 8 of the dendrogram. The spring-run population returning to the Lewis River lies geographically within unit V, entering the Columbia River below Bonneville Dam. This population is included in unit VI because it is genetically distinct from other downstream populations and more typical of certain spring- and fall-run fish within Unit VI (i.e., Klickitat, Deschutes, and Winthrop populations) with which it closely aggregates on the dendrogram (cluster 8C) and the plots of PC1 and PC2.

The similarity of the populations from Wells Dam and Priest Rapids Dam in unit VI is presumably a reflection of the two groups being different temporal segments of the same major run. All fish migrating past Priest Rapids Dam prior to 13 August are permitted to pass upstream and sequentially constitute the spring- and summer-runs of the upper Columbia River. The latter segment of this migration arriving at Wells Dam is captured and spawned for hatchery production. Most arrivals at Priest Rapids Dam later than 14 August are intercepted and spawned there (Chris Carlson[7]). This process inevitably results in considerable gene flow between these two artificially maintained populations.

The Snake River unit (unit VII) contains the two combined populations of McCall Hatchery-Johnson Creek and Rapid River Hatchery-Valley Creek-Sawtooth-Red River, all managed by the Idaho Department of Fish and Game; all populations are from the Salmon River drainage of central Idaho. This unit is distinguished by very low average heterozygosities (see Winans in press) and by high frequencies of the *Pgk-2 (90)* allele.

The Klamath River populations (unit VIII) are geographically isolated from, but genetically similar to those of the Snake River. However, populations of unit VIII lack variation of Idh-3,4 contrasted with a mean frequency of 0.925 for the *Idh-3,4 (100)* allele in unit VII. Klamath River populations, like those of unit VII, are characterized by very low average heterozygosities. This characteristic contrasts sharply with most adjacent coastal populations for which the highest heterozygosities among all populations are observed. Allele frequency data from the Shasta and Scott river populations, two wild populations of the Klamath River are statistically identical with frequencies in the Iron Gate Hatchery sample; these data were recently collected which precluded their use in most of the analyses of this study. Thus the low heterozygosity of Klamath River populations cannot be attributed to effects of hatchery management (see Allendorf and Ryman 1987).

The three samples from the Sacramento River drainage form a distinct geographic and genetic unit (unit IX). These samples cluster together in the dendrogram (cluster 7) and in PC1 and PC2. As mentioned above, these populations are distinguished by high frequencies of the *Gpi-1(H)* allele.

An analysis of gene diversity within and between the nine proposed population units (Table 5, column 3), provides further support for the reality of these genetic subdivisions. It is appropriate that almost two-thirds of the total gene diversity due to population structuring (7.9/12.3 = 64.2%) occurred between the population units. Furthermore, the diversity between populations within the units was smaller than the diversity between populations within areas (Table 5, column 1) calculated prior to the synthesis of the units.

Relationships and Origins of Population Units

The common genetic and geographic attributes of populations within units have been stressed, but relationships between units also require consideration. The geographic areas of the Fraser River, Georgia Strait, and Puget Sound (units I, II, and III) were completely glaciated during the late Pleistocene, and therefore must have been entirely repopulated within roughly the last 15,000 years (McPhail and Lindsey 1986). Those areas of the Columbia River sampled in this study were outside of the ice sheet, although the upper third of the drainage was glaciated. However, downstream populations (units V and VI) were doubtlessly affected by massive runoffs and temporary impoundments resulting from sudden releases of glacial Lake Missoula initially occurring some 18,000 years ago (Bunker 1982); most of the Snake River drainage (unit VII), entering the mid-Columbia River from the south, was presumably unaffected by these events above its lower reaches. The coastal region (Unit IV) from the Chehalis River (Washington) southward, and the entire Sacramento-San Joaquin River drainage (unit III), were likewise free of glaciation during the late Pleistocene.

Much of the presently observed genetic diversity almost certainly existed during the Pleistocene. The

[7]Chris Carlson, Grant County Public Utility District, P.O. Box 878, Ephrata, WA 98823, pers. commun. March 1986.

broad geographic range and high heterozygosity of the coastal populations support the long-term existence of unit IV in which cohesiveness among populations appears to have been maintained through some degree of gene flow (Soule 1976; Campton and Utter 1987). Ecological as well as geographic barriers to extensive gene flow from the coastal area apparently existed in the Columbia, Klamath, and Sacramento drainages. However, the presence of the *Gpi-2(60)* allele—typical of coastal populations—in some populations of units V, VI, VIII, and IX suggests some degree of introgression from coastal populations. Natural obstructions of the mid-Columbia River such as Cascade Falls and Celilo Falls (presently obscured by Bonneville and The Dalles Dams, respectively) may have restricted migration between populations of the lower Columbia River and those of the upper Columbia and Snake Rivers.

The relationship of the Snake River populations of unit VII to other groups within and beyond the Columbia River is unclear. Its most distinguishing feature is its very low average heterozygosity ($\bar{H}$ = 0.04), an attribute shared with the Klamath River populations ($\bar{H}$ = 0.029) (unit VIII) with which it also aggregates in the dendrogram and the principal component projections. In spite of this similarity, we favor an explanation that both Snake River and Klamath River populations had independent origins. The high frequencies of common (i.e., 100) alleles over the present sampling of loci are interpreted as reflecting loss of variation through genetic drift accentuated by periodic bottlenecks and restricted gene flow (see also Winans in press). This explanation is consistent with the inland locations of both drainages. In addition, both drainages continued to flow within their present courses during the Pleistocene. Thus, similarity is presently interpreted as an artifact based on minimal allelic variation detected over most of the loci sampled. However, drift coupled with isolation should lead to divergent frequencies of some alternate alleles with an adequate sampling of variable loci. If such differences are not observed as additional genetic marks continue to be detected in chinook salmon, then a zoogeographical explanation based on gene flow or recent ancestry must be pursued for Snake River and Klamath River populations.

Following glacial regression, the newly habitable regions appear to have been repopulated from diverse sources. Origins of the northern portions of the coastal unit can be readily explained by immigrations from more southern coastal streams. However, populations of units I, II, and III apparently arose from other sources based on their virtual absence of Gpi-2 variation. Seeding of the Fraser River from sources including the upper Columbia River and Snake River units, and of Georgia Strait and Puget Sound drainages from the lower Columbia River or Alaska, are possibilities that seem more likely. The *Aat-3 (85)* allele is recorded in most Alaskan populations studied by Gharrett et al. (1987) at frequencies up to 0.32. The highest frequencies of this allele occur in populations from Vancouver Island suggesting immigration from northern refugia.

Comparisons with Sympatric Salmonid Species

It is of interest to compare the present data set with similar information from other anadromous salmonid species within the same geographic range. These species presently share habitats and have been subjected to the same geological processes throughout their periods of common habitation. Thus, some common patterns of genetic population structuring may be anticipated. However, differences among species in life histories and long-term distributions may likewise result in unique population structures. Similar data sets have been collected from four species within this range: rainbow trout, *Salmo gairdneri*; coastal cutthroat trout, *S. clarki*; chum salmon, *O. keta*; and sockeye salmon, *O. nerka*.

Investigations of rainbow trout include both anadromous (i.e., steelhead) and nonmigratory populations (Huzyk and Tsuyuki 1974; Allendorf 1975; Allendorf and Utter 1979; Allendorf et al. 1980; Busack et al. 1980; Chilcote et al. 1980; Parkinson 1984; Wishard et al. 1984). A geographic basis for population structure is also apparent in this species and allelic similarities persist among indigenous populations of a particular region regardless of migratory tendencies, times of migration, or local environments. Apparent population units for chinook salmon and rainbow trout differ, however. A single major population unit of rainbow trout comprising the upper Fraser River, the upper Columbia River, and the Snake River contrasts with at least three distinct groupings for chinook salmon. A clear distinction between coastal streams of Washington and Oregon from those of the lower Columbia River, Puget Sound, and Georgia Strait is also not apparent in rainbow trout as it is in chinook salmon.

Distribution of sockeye salmon over the geographic range of this study is less continuous than that of chinook salmon because of the more stringent

ecological requirements of sockeye salmon during their freshwater life history. This irregular distribution is accompanied by greater geographic heterogeneity of allelic distributions, perhaps reflecting severe founder events and restricted gene flow (Utter et al. 1984). One population of sockeye salmon on the Quinault River (Washington coast) deviated strongly from all other groups sampled, but the possibility of a coastal unit of sockeye salmon, analogous to that of chinook salmon (i.e., unit IV), appears unlikely. Allele frequencies from Lake Ozette on the Washington coast (W. K. Hershberger[8]) were typical of noncoastal populations. Populations north of the Skeena River (approximately the position of "A" in Figure 1) are distinguished by the presence of Ldh-4 variation which is virtually absent from more southern groups (Utter et al. 1980; Withler 1985), presumably reflecting postglacial repopulation from a more northern refuge.

Studies of population groups of chum salmon and coastal cutthroat trout within Puget Sound and Georgia Stait suggest similar genetic structures to that observed in chinook salmon. Populations of chum salmon from south Puget Sound were distinguishable from those of north Puget Sound and Georgia Strait (Okazaki 1981). Populations of Georgia Strait and the lower Fraser River were likewise distinguishable from populations immediately north of Georgia Strait (Beacham et al. 1985). Intensive subsampling of cutthroat trout within Hood Canal and north Puget Sound indicated strong and consistent differences between these regions (Campton and Utter 1987).

More comprehensive comparisons will be possible as data accumulate on these and other species of anadromous salmonids. Both the similarities and the differences observed are of considerable interest in gaining further insights into the determinants of allele frequency variation, zoogeography, behavior, and management of these species.

Effects of Hatchery Operations

Further consideration of the effects of hatchery operations is also warranted. Hatchery operations and transplanted hatchery fish do not appear to have drastically altered the geographic distributions of protein coding alleles among the major population units. There is presently little question that hatchery operations have homogenized allele frequencies among many fall chinook hatcheries of the lower Columbia River (Simon 1972). However, the temporally isolated spring and fall populations of this region retain a greater similarity to one another than to populations of other regions. Thus it seems probable that the allele frequencies of unit V approximate those existing prior to the present century in spite of this region's large predominance of hatchery fish. Hatchery populations established from (and still reflecting) exotic origins (e.g., Carson and Leavenworth Hatcheries) have not noticeably perturbed the allelic distributions of adjacent populations having indigenous origins (Utter et al. 1987[9]). Where they exist (e.g., unit IV), indigenous wild and hatchery populations within a unit are generally separated by small genetic distances, reflected by close aggregations in the dendrogram and principal component clusters.

Infrequent alleles do not strongly affect genetic distance or heterozygosity, but their loss in hatchery stocks relative to comparable wild populations is a good indication of an inadequate number of spawning individuals used to establish or maintain a hatchery stock (Allendorf and Ryman 1987). A comparison was therefore made of the average number of alleles per locus and heterozygosity between seven hatchery and six wild samples from the Oregon coast, the most extensive collection of hatchery and wild samples within a restricted geographic range made in this study (two statistically indistinguishable combined populations each involving a hatchery and a wild sample were excluded). The mean values were very similar (heterozygosity—hatchery 0.137, wild 0.132; alleles per locus—hatchery 1.74, wild 1.68) and were not significantly different. Presumably, sufficient numbers of breeders have been used in Oregon coastal hatcheries to prevent losses of heterozygosity or alleles. However, the data provide no information concerning possible losses of genetically distinct geographic or temporal segments as a result of hatchery practices along the Oregon coast.

The present data set also pertains to additional aspects of hatchery management. Evidence continues to accumulate from numerous sources that individual populations of anadromous salmonids represent gene pools that are uniquely adapted to a particular location and spawning time (see Ricker 1972). Stocks transferred to areas beyond those to which they are locally adapted perform poorly

[8]W. K. Hershberger, Univ. of Washington, Seattle, WA 98195, pers. commun. December 1985.

[9]Utter, F., P. Aebersold, M. Griswold, G. Milner, N. Putas, J. Szeles, D. Teel, and G. Winans. 1987. Biochemical genetic variation of chinook salmon stocks of the mid-Columbia River. Processed Report 87-19, 22 p. Northwest and Alaska Fisheries Center, Seattle, WA 98112.

relative to indigenous populations (Withler 1982; Altukhov and Salmenkova 1987; Reisenbichler 1988). Transfers from maladapted populations not only waste effort and resource, but also carry the risk of disrupting locally adapted genomes through interbreedings (Reisenbichler and McIntyre 1977; Shields 1982). Sets of data such as those reported here are valuable in outlining at least the maximum distribution of locally adapted gene pools and thereby provide guidelines for stock transfers. In the absence of any other data, it would be inadvisable to translocate populations between sites such as the lower Columbia River and the Washington or Oregon coasts.

Stock transfers within major genetic units should also be performed with caution. Each of the individual or pooled populations within the nine units is also genetically distinct for some loci sampled in this study from other populations within the unit; they are therefore divergent from such populations at a much larger number of additional loci throughout the genome. It is pertinent to recall that a considerable amount of the total gene diversity results from population subdivision (4.4/12.3 = 35.8%) resided within the population units (Table 5, column 3). Likewise, slight or no divergence between two populations based on samplings of polymorphic protein-coding loci does not necessarily mean these populations are identically adapted (discussed in Utter 1981). For example, two groups of rainbow trout in the Snake River drainage having similar allele frequencies at five polymorphic loci are adapted to drastically different local environments and life history patterns (Wishard et al. 1984).

CONCLUDING OBSERVATIONS

Three points require emphasis following this initial outline of population units. First, it warrants restating that each of the nine units represents a genetically heterogeneous grouping. It is important that this heterogeneity be recognized and maintained within the respective units.

Second, these units are based on limited data within the range of sampling and, in some instances, on arbitrary decisions; the units are intended to be modified as more information accumulates and therefore to serve as guidelines for further investigation. For purposes of clarification, allelic data beyond those listed in the Appendix have been introduced at various places in the text. Additional alleles and polymorphic protein-coding loci are continually being identified through ongoing investigations, and further clarification is inevitable as these data accumulate. Genetic data other than from protein-coding loci are accumulating on chinook salmon populations within the geographic range of this study. Such genetic data show differences among populations in mitochondrial DNA (E. Bermingham[10]), and life history variables (Nicholas and Hankin 1988; Schreck et al. 1986), and provide complementary insights that will ultimately result in a much more detailed understanding of genetic structuring of these chinook salmon populations.

Third, numerous distinct population units exist in North America beyond the sampling area of this study (e.g., Gharrett et al. 1987) and nothing is known of Asiatic populations. The nine units presented here, then, are viewed as a necessary part of a much more complete picture of the genetic structure of chinook salmon that will ultimately emerge.

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APPENDIX A

Allele frequencies and average heterozygosities for 65 individual and pooled populations of naturally reproducing and hatchery stocks of chinook salmon. Hatchery stocks are identified by (\$). The map code refers to Figure 1.

Appendix A.—*Continued.*

Map code	Population	Locus and alleles								
		Ah					Ada-1		Aat-1,2	
		100	86	116	108	69	100	83	100	85
A1	Babine	0.986	0.014	0	0	0	0.986	0.014	1.000	0
B1	Tete Jaune	0.882	0.118	0	0	0	0.986	0.014	1.000	0
B2	Clearwater	0.786	0.214	0	0	0	0.900	0.100	1.000	0
B3	Chilco	0.922	0.078	0	0	0	0.969	0.031	1.000	0
B4	Stuart–Nechako	0.958	0.042	0	0	0	0.894	0.106	1.000	0
C1	$Big Qualicum	0.838	0.162	0	0	0	0.953	0.047	1.000	0
C2	$Puntledge	0.610	0.390	0	0	0	0.975	0.025	0.990	0.010
C3	$Quinsam	0.366	0.629	0.005	0	0	0.995	0.005	0.997	0.003
C4	$San Juan	0.820	0.160	0	0.020	0	1.000	0	0.987	0.013
C5	$Capilano	0.763	0.237	0	0	0	0.909	0.091	0.967	0.033
C6	Nooksack SF	0.780	0.220	0	0	0	0.870	0.130	0.995	0.005
C7	Nooksack NF	0.810	0.190	0	0	0	0.927	0.073	0.922	0.078
D1	$Robertson Ck.	0.806	0.194	0	0	0	1.000	0	0.981	0.019
E1	$Wells Dam	0.800	0.200	0	0	0	1.000	0	1.000	0
E2	$Carson–$Leavenworth	0.987	0.010	0.003	0	0	0.969	0.031	1.000	0
E3	$Winthrop	0.920	0.070	0.010	0	0	0.973	0.027	1.000	0
E4	$Priest Rapids	0.825	0.175	0	0	0	0.985	0.015	1.000	0
F1	$Soleduck (sum)	0.959	0.036	0.005	0	0	1.000	0	0.929	0.071
F2	$Soleduck (spr)	0.848	0.152	0	0	0	0.995	0.005	0.998	0.003
F3	$Naselle	0.908	0.092	0	0	0	0.980	0.020	0.965	0.035
F4	$Humptulips	0.920	0.080	0	0	0	1.000	0	0.975	0.025
F5	$Quinault	0.920	0.080	0	0	0	0.985	0.015	0.975	0.025
F6	Queets	0.959	0.032	0.009	0	0	0.985	0.015	0.994	0.006
F7	Hoh	0.930	0.040	0.030	0	0	1.000	0	0.994	0.006
F8	$Soleduck (f)	0.837	0.133	0.031	0	0	1.000	0	1.000	0
F9	$Elwha	0.920	0.080	0	0	0	0.980	0.020	1.000	0
G1	$Skykomish	0.860	0.135	0.005	0	0	0.865	0.135	0.980	0.020
G2	$Skagit	0.838	0.162	0	0	0	0.959	0.041	0.985	0.015
G3	$Hood Canal	0.918	0.077	0.005	0	0	0.903	0.097	0.888	0.112
G4	$Deschutes	0.842	0.158	0	0	0	0.953	0.047	0.913	0.088
G5	$Green R.–$Sammish	0.903	0.097	0	0	0	0.973	0.027	0.966	0.034
H1	$Cowlitz–$Kalama	0.845	0.149	0.006	0	0	0.975	0.025	1.000	0
H2	$Lewis R. (spr)	0.910	0.080	0	0	0.010	0.980	0.020	0.995	0.005
H3	$Cowlitz–$Kalama	0.855	0.131	0.014	0	0	0.993	0.007	1.000	0
H4	$Lewis R. (f)	0.800	0.200	0	0	0	0.980	0.020	1.000	0
H5	$Washougal R.	0.850	0.120	0.030	0	0	1.000	0	0.995	0.005
H6	$Eagle Ck.–$McKenzie R.	0.782	0.190	0.029	0	0	1.000	0	1.000	0
I1	$Klickitat R.	0.930	0.070	0	0	0	0.980	0.020	0.995	0.005
I2	$Spring Ck.–$Big Ck.	0.990	0.010	0	0	0	1.000	0	1.000	0
I3	$Warm Spr.–$Round Butte	1.000	0	0	0	0	1.000	0	0.996	0.004
I4	Deschutes	0.867	0.102	0.031	0	0	0.990	0.010	1.000	0
J1	Ice Harbor	0.874	0.111	0.003	0.013	0	0.998	0.003	1.000	0
J2	McCall–Johnson Ck.	1.000	0	0	0	0	0.953	0.047	0.981	0.019
J3	$Rapid R.–Valley Ck.	0.994	0.006	0	0	0	0.969	0.031	0.997	0.003
K1	$Cole R.–Hoot Owl Ck.	0.957	0.043	0	0	0	1.000	0	0.998	0.002
K2	$Rock Ck.	0.890	0.105	0.005	0	0	1.000	0	0.990	0.010
K3	$Cedar Ck.	0.760	0.087	0.036	0.010	0.107	1.000	0	0.987	0.013
K4	$Trask R. (spr)	0.735	0.110	0.020	0.020	0.115	1.000	0	0.978	0.023
K5	Chetco	0.890	0.110	0	0	0	0.990	0.010	0.990	0.010
K6	Lobster Ck.	0.930	0.070	0	0	0	1.000	0	0.975	0.025
K7	$Elk R.	0.800	0.185	0.015	0	0	0.950	0.050	0.950	0.050
K8	Sixes R. estu.	0.850	0.105	0.035	0.010	0	0.985	0.015	0.968	0.032
K9	Coquille R. estu.	0.883	0.113	0	0.004	0	0.965	0.035	0.949	0.051
K10	Siuslaw Bay	0.790	0.136	0.049	0.006	0.019	0.976	0.024	0.959	0.041
K11	$Salmon R.	0.737	0.076	0.152	0.035	0	1.000	0	0.990	0.010
K12	$Nestucca R.–$Alsea R.	0.811	0.064	0.113	0.001	0.012	0.969	0.031	0.976	0.024
K13	$Cedar Ck.	0.610	0.215	0.120	0	0.055	0.995	0.005	0.944	0.056
K14	$Trask R.–Tillamook Bay	0.730	0.141	0.113	0.003	0.013	0.968	0.032	0.991	0.009
K15	Nehalem estu.	0.685	0.236	0.079	0	0	0.984	0.016	0.990	0.010
L1	$Feather R.	0.720	0.240	0.040	0	0	1.000	0	1.000	0
L2	$Coleman–$Nimbus	0.815	0.173	0.007	0.005	0	1.000	0	0.992	0.008
L3	$Feather R.–$Mokelumne	0.797	0.195	0.005	0.002	0	1.000	0	0.999	0.001
M1	$Trinity R.	1.000	0	0	0	0	1.000	0	1.000	0
M2	$Iron Gate	0.995	0	0	0.005	0	1.000	0	0.997	0.003
M3	$Trinity (f)	1.000	0	0	0	0	1.000	0	1.000	0

Appendix A.—*Continued.*

Map code	Population	Locus and alleles								
		Aat-3		Dpep-1		Dpep-2		Gpi-1		
		100	90	100	90	100	105	100	60	H
A1	Babine	0.957	0.043	0.972	0.028	1.000	0	1.000	0	0
B1	Tete Jaune	1.000	0	0.987	0.013	1.000	0	1.000	0	0
B2	Clearwater	1.000	0	1.000	0	1.000	0	1.000	0	0
B3	Chilco	1.000	0	0.979	0.021	0.939	0.061	1.000	0	0
B4	Stuart–Nechako	1.000	0	0.963	0.037	1.000	0	1.000	0	0
C1	$Big Qualicum	0.829	0.171	0.935	0.065	1.000	0	1.000	0	0
C2	$Puntledge	0.735	0.265	0.995	0.005	1.000	0	1.000	0	0
C3	$Quinsam	0.831	0.169	0.974	0.026	1.000	0	1.000	0	0
C4	$San Juan	0.990	0.010	0.970	0.030	1.000	0	1.000	0	0
C5	$Capilano	0.803	0.197	0.985	0.015	1.000	0	1.000	0	0
C6	Nooksack SF	0.990	0.010	0.918	0.082	1.000	0	1.000	0	0
C7	Nooksack NF	1.000	0	0.980	0.020	1.000	0	1.000	0	0
D1	$Robertson Ck.	0.911	0.089	1.000	0	1.000	0	1.000	0	0
E1	$Wells Dam	1.000	0	0.980	0.020	1.000	0	0.859	0	0.141
E2	$Carson–$Leavenworth	1.000	0	0.993	0.007	1.000	0	1.000	0	0
E3	$Winthrop	1.000	0	1.000	0	1.000	0	1.000	0	0
E4	$Priest Rapids	1.000	0	0.995	0.005	1.000	0	0.824	0	0.176
F1	$Soleduck (sum)	0.995	0.005	0.745	0.255	1.000	0	1.000	0	0
F2	$Soleduck (spr)	0.995	0.005	0.970	0.030	1.000	0	1.000	0	0
F3	$Naselle	1.000	0	0.843	0.157	0.995	0.005	1.000	0	0
F4	$Humptulips	1.000	0	0.840	0.160	1.000	0	1.000	0	0
F5	$Quinault	1.000	0	0.890	0.110	1.000	0	0.995	0.005	0
F6	Queets	1.000	0	0.833	0.167	0.954	0.046	0.996	0.004	0
F7	Hoh	1.000	0	0.905	0.095	0.995	0.005	0.980	0.020	0
F8	$Soleduck (f)	1.000	0	0.740	0.260	1.000	0	1.000	0	0
F9	$Elwha	0.979	0.021	0.890	0.110	1.000	0	1.000	0	0
G1	$Skykomish	0.967	0.033	0.980	0.020	1.000	0	1.000	0	0
G2	$Skagit	1.000	0	0.925	0.075	1.000	0	1.000	0	0
G3	$Hood Canal	0.995	0.005	0.923	0.077	1.000	0	1.000	0	0
G4	$Deschutes	1.000	0	0.893	0.107	1.000	0	1.000	0	0
G5	$Green R.–$Sammish	1.000	0	0.876	0.124	1.000	0	1.000	0	0
H1	$Cowlitz–$Kalama	1.000	0	0.949	0.051	1.000	0	0.895	0	0.105
H2	$Lewis R. (spr)	1.000	0	1.000	0	1.000	0	1.000	0	0
H3	$Cowlitz–$Kalama	1.000	0	0.913	0.087	1.000	0	1.000	0	0
H4	$Lewis R. (f)	1.000	0	0.830	0.170	1.000	0	1.000	0	0
H5	$Washougal R.	1.000	0	0.850	0.150	0.990	0.010	1.000	0	0
H6	$Eagle Ck.–$McKenzie R.	1.000	0	1.000	0	1.000	0	1.000	0	0
I1	$Klickitat R.	1.000	0	0.990	0.010	1.000	0	1.000	0	0
I2	$Spring Ck.–$Big Ck.	1.000	0	0.987	0.013	1.000	0	1.000	0	0
I3	$Warm Spr.–$Round Butte	1.000	0	0.972	0.028	1.000	0	1.000	0	0
I4	Deschutes	0.989	0.011	0.898	0.102	1.000	0	1.000	0	0
J1	Ice Harbor	0.996	0.004	0.967	0.033	1.000	0	0.842	0	0.158
J2	McCall–Johnson Ck.	1.000	0	1.000	0	1.000	0	1.000	0	0
J3	$Rapid R.–Valley Ck.	1.000	0	0.994	0.006	1.000	0	1.000	0	0
K1	$Cole R.–Hoot Owl Ck.	0.972	0.028	0.908	0.092	1.000	0	0.890	0	0.110
K2	$Rock Ck.	0.955	0.045	0.925	0.075	1.000	0	1.000	0	0
K3	$Cedar Ck.	0.995	0.005	0.652	0.348	1.000	0	1.000	0	0
K4	$Trask R. (spr)	0.995	0.005	0.783	0.217	1.000	0	1.000	0	0
K5	Chetco	1.000	0	0.855	0.145	1.000	0	1.000	0	0
K6	Lobster Ck.	1.000	0	0.850	0.150	1.000	0	1.000	0	0
K7	$Elk R.	1.000	0	0.732	0.268	1.000	0	1.000	0	0
K8	Sixes R. estu.	1.000	0	0.655	0.345	1.000	0	1.000	0	0
K9	Coquille R. estu.	1.000	0	0.652	0.348	1.000	0	1.000	0	0
K10	Siuslaw Bay	1.000	0	0.701	0.299	1.000	0	1.000	0	0
K11	$Salmon R.	0.995	0.005	0.783	0.217	1.000	0	1.000	0	0
K12	$Nestucca R.–$Alsea R.	0.999	0.001	0.708	0.292	1.000	0	1.000	0	0
K13	$Cedar Ck.	0.995	0.005	0.700	0.300	1.000	0	1.000	0	0
K14	$Trask R.–Tillamook Bay	1.000	0	0.704	0.296	1.000	0	1.000	0	0
K15	Nehalem estu.	0.980	0.020	0.770	0.230	1.000	0	1.000	0	0
L1	$Feather R.	1.000	0	0.890	0.110	1.000	0	0.576	0	0.424
L2	$Coleman–$Nimbus	1.000	0	0.869	0.131	1.000	0	0.705	0	0.295
L3	$Feather R.–$Mokelumne	1.000	0	0.905	0.095	1.000	0	0.689	0	0.311
M1	$Trinity R.	1.000	0	0.990	0.010	1.000	0	1.000	0	0
M2	$Iron Gate	1.000	0	0.995	0.005	1.000	0	1.000	0	0
M3	$Trinity (f)	1.000	0	1.000	0	1.000	0	1.000	0	0

Appendix A.—*Continued.*

Map code	Population	Locus and alleles						
		Gpi-2		Gpi-3			Gr	
		100	60	100	105	93	100	85
A1	Babine	1.000	0	0.917	0.083	0	0.973	0.027
B1	Tete Jaune	1.000	0	0.932	0.068	0	0.958	0.042
B2	Clearwater	1.000	0	0.989	0.011	0	0.856	0.144
B3	Chilco	1.000	0	0.875	0.125	0	0.939	0.061
B4	Stuart–Nechako	1.000	0	0.933	0.067	0	0.860	0.140
C1	$Big Qualicum	1.000	0	1.000	0	0	1.000	0
C2	$Puntledge	1.000	0	0.995	0.005	0	1.000	0
C3	$Quinsam	1.000	0	1.000	0	0	0.995	0.005
C4	$San Juan	1.000	0	1.000	0	0	0.970	0.030
C5	$Capilano	1.000	0	1.000	0	0	1.000	0
C6	Nooksack SF	1.000	0	0.880	0.120	0	0.990	0.010
C7	Nooksack NF	1.000	0	0.950	0.050	0	0.908	0.092
D1	$Robertson Ck.	0.755	0.245	1.000	0	0	1.000	0
E1	$Wells Dam	1.000	0	0.970	0.030	0	0.980	0.020
E2	$Carson–$Leavenworth	1.000	0	1.000	0	0	0.993	0.007
E3	$Winthrop	1.000	0	0.984	0.016	0	0.918	0.082
E4	$Priest Rapids	1.000	0	1.000	0	0	0.975	0.025
F1	$Soleduck (sum)	0.613	0.387	1.000	0	0	1.000	0
F2	$Soleduck (spr)	1.000	0	1.000	0	0	1.000	0
F3	$Naselle	0.788	0.212	1.000	0	0	1.000	0
F4	$Humptulips	0.755	0.245	0.970	0	0.030	0.990	0.010
F5	$Quinault	0.700	0.300	0.980	0.020	0	1.000	0
F6	Queets	0.671	0.329	0.996	0.004	0	1.000	0
F7	Hoh	0.542	0.458	0.995	0.005	0	1.000	0
F8	$Soleduck (f)	0.553	0.447	0.980	0.020	0	1.000	0
F9	$Elwha	0.684	0.316	0.975	0.025	0	0.995	0.005
G1	$Skykomish	1.000	0	0.955	0.045	0	0.995	0.005
G2	$Skagit	1.000	0	0.995	0.005	0	1.000	0
G3	$Hood Canal	1.000	0	1.000	0	0	1.000	0
G4	$Deschutes	0.916	0.084	0.990	0.010	0	1.000	0
G5	$Green R.–$Sammish	1.000	0	0.993	0.003	0.003	0.990	0.010
H1	$Cowlitz–$Kalama	1.000	0	1.000	0	0	0.822	0.179
H2	$Lewis R. (spr)	1.000	0	1.000	0	0	0.908	0.092
H3	$Cowlitz–$Kalama	0.916	0.084	1.000	0	0	0.795	0.205
H4	$Lewis R. (f)	1.000	0	1.000	0	0	0.820	0.180
H5	$Washougal R.	1.000	0	1.000	0	0	0.800	0.200
H6	$Eagle Ck.–$McKenzie R.	1.000	0	1.000	0	0	0.420	0.580
I1	$Klickitat R.	1.000	0	1.000	0	0	0.760	0.240
I2	$Spring Ck.–$Big Ck.	1.000	0	1.000	0	0	0.663	0.337
I3	$Warm Spr.–$Round Butte	1.000	0	1.000	0	0	1.000	0
I4	Deschutes	1.000	0	0.990	0	0.010	0.949	0.051
J1	Ice Harbor	0.929	0.071	1.000	0	0	1.000	0
J2	McCall–Johnson Ck.	1.000	0	1.000	0	0	1.000	0
J3	$Rapid R.–Valley Ck.	1.000	0	1.000	0	0	1.000	0
K1	$Cole R.–Hoot Owl Ck.	0.842	0.158	1.000	0	0	0.997	0.003
K2	$Rock Ck.	0.755	0.245	1.000	0	0	0.925	0.075
K3	$Cedar Ck.	0.698	0.302	1.000	0	0	1.000	0
K4	$Trask R. (spr)	0.553	0.447	1.000	0	0	0.961	0.039
K5	Chetco	0.827	0.173	1.000	0	0	1.000	0
K6	Lobster Ck.	1.000	0	1.000	0	0	0.960	0.040
K7	$Elk R.	0.520	0.480	1.000	0	0	1.000	0
K8	Sixes R. estu.	0.434	0.566	1.000	0	0	1.000	0
K9	Coquille R. estu.	0.441	0.559	0.991	0.009	0	1.000	0
K10	Siuslaw Bay	0.545	0.455	1.000	0	0	1.000	0
K11	$Salmon R.	0.682	0.318	1.000	0	0	1.000	0
K12	$Nestucca R.–$Alsea R.	0.525	0.475	0.997	0.003	0	1.000	0
K13	$Cedar Ck.	0.432	0.568	1.000	0	0	1.000	0
K14	$Trask R.–Tillamook Bay	0.435	0.565	1.000	0	0	1.000	0
K15	Nehalem estu.	0.783	0.217	1.000	0	0	1.000	0
L1	$Feather R.	1.000	0	1.000	0	0	1.000	0
L2	$Coleman–$Nimbus	0.945	0.055	1.000	0	0	1.000	0
L3	$Feather R.–$Mokelumne	0.900	0.100	1.000	0	0	1.000	0
M1	$Trinity R.	0.859	0.141	1.000	0	0	1.000	0
M2	$Iron Gate	1.000	0	1.000	0	0	0.995	0.005
M3	$Trinity (f)	1.000	0	1.000	0	0	1.000	0

Appendix A.—*Continued.*

Map code	Population	Locus and alleles: Idh-3,4 100	Idh-3,4 127	Idh-3,4 74	Idh-3,4 142	Ldh-4 100	Ldh-4 112	Ldh-4 134	Ldh-4 71
A1	Babine	0.947	0.007	0.046	0	1.000	0	0	0
B1	Tete Jaune	1.000	0	0	0	1.000	0	0	0
B2	Clearwater	0.967	0.006	0.011	0.017	0.933	0	0	0.067
B3	Chilco	0.985	0.005	0.010	0	1.000	0	0	0
B4	Stuart–Nechako	0.976	0.009	0.002	0.012	1.000	0	0	0
C1	$Big Qualicum	1.000	0	0	0	1.000	0	0	0
C2	$Puntledge	0.995	0.005	0	0	1.000	0	0	0
C3	$Quinsam	1.000	0	0	0	1.000	0	0	0
C4	$San Juan	1.000	0	0	0	1.000	0	0	0
C5	$Capilano	0.970	0.013	0.018	0	1.000	0	0	0
C6	Nooksack SF	0.984	0.016	0	0	1.000	0	0	0
C7	Nooksack NF	1.000	0	0	0	1.000	0	0	0
D1	$Robertson Ck.	0.980	0.020	0	0	1.000	0	0	0
E1	$Wells Dam	0.875	0.125	0	0	1.000	0	0	0
E2	$Carson–$Leavenworth	0.862	0.002	0.136	0	0.973	0.027	0	0
E3	$Winthrop	0.965	0.010	0.025	0	0.996	0.004	0	0
E4	$Priest Rapids	0.908	0.090	0.003	0	1.000	0	0	0
F1	$Soleduck (sum)	0.874	0.111	0.003	0.013	1.000	0	0	0
F2	$Soleduck (spr)	0.958	0.037	0.005	0	1.000	0	0	0
F3	$Naselle	0.987	0.010	0	0.003	1.000	0	0	0
F4	$Humptulips	0.985	0.010	0	0.005	1.000	0	0	0
F5	$Quinault	0.903	0.090	0.003	0.005	1.000	0	0	0
F6	Queets	0.892	0.108	0	0	1.000	0	0	0
F7	Hoh	0.908	0.093	0	0	1.000	0	0	0
F8	$Soleduck (f)	0.990	0.010	0	0	1.000	0	0	0
F9	$Elwha	0.898	0.095	0.003	0.005	1.000	0	0	0
G1	$Skykomish	0.958	0.008	0	0.035	1.000	0	0	0
G2	$Skagit	0.960	0.010	0.010	0.020	1.000	0	0	0
G3	$Hood Canal	0.957	0.003	0.005	0.036	1.000	0	0	0
G4	$Deschutes	0.942	0.055	0.003	0	1.000	0	0	0
G5	$Green R.–$Sammish	0.968	0.009	0.002	0.022	1.000	0	0	0
H1	$Cowlitz–$Kalama	0.915	0.055	0.030	0	1.000	0	0	0
H2	$Lewis R. (spr)	0.925	0.005	0.070	0	0.980	0.020	0	0
H3	$Cowlitz–$Kalama	0.971	0.012	0.017	0	1.000	0	0	0
H4	$Lewis R. (f)	0.933	0.022	0.044	0	1.000	0	0	0
H5	$Washougal R.	0.955	0.015	0.030	0	1.000	0	0	0
H6	$Eagle Ck.–$McKenzie R.	0.868	0.126	0.006	0	1.000	0	0	0
I1	$Klickitat R.	0.900	0.070	0.030	0	1.000	0	0	0
I2	$Spring Ck.–$Big Ck.	0.990	0.008	0.002	0	1.000	0	0	0
I3	$Warm Spr.–$Round Butte	0.865	0	0.135	0	1.000	0	0	0
I4	Deschutes	0.969	0.031	0	0	1.000	0	0	0
J1	Ice Harbor	0.977	0.023	0	0	1.000	0	0	0
J2	McCall–Johnson Ck.	0.913	0	0.087	0	1.000	0	0	0
J3	$Rapid R.–Valley Ck.	0.937	0.006	0.057	0	0.972	0.028	0	0
K1	$Cole R.–Hoot Owl Ck.	0.962	0.038	0	0	0.994	0.003	0.003	0
K2	$Rock Ck.	0.977	0.023	0	0	1.000	0	0	0
K3	$Cedar Ck.	0.995	0.003	0.003	0	1.000	0	0	0
K4	$Trask R. (spr)	0.995	0.005	0	0	1.000	0	0	0
K5	Chetco	0.985	0.015	0	0	1.000	0	0	0
K6	Lobster Ck.	0.978	0.022	0	0	0.940	0	0.060	0
K7	$Elk R.	0.973	0.027	0	0	0.990	0	0	0.010
K8	Sixes R. estu.	0.972	0.028	0	0	0.970	0.005	0.010	0.015
K9	Coquille R. estu.	1.000	0	0	0	0.961	0	0.003	0.009
K10	Siuslaw Bay	0.994	0.003	0.003	0	1.000	0	0	0
K11	$Salmon R.	0.975	0.025	0	0	1.000	0	0	0
K12	$Nestucca R.–$Alsea R.	0.981	0.016	0.001	0.001	0.999	0	0	0.001
K13	$Cedar Ck.	0.947	0.053	0	0	1.000	0	0	0
K14	$Trask R.–Tillamook Bay	0.963	0.037	0	0	1.000	0	0	0
K15	Nehalem estu.	0.947	0.053	0	0	1.000	0	0	0
L1	$Feather R.	0.940	0.060	0	0	1.000	0	0	0
L2	$Coleman–$Nimbus	0.950	0.050	0	0	1.000	0	0	0
L3	$Feather R.–$Mokelumne	0.945	0.055	0	0	1.000	0	0	0
M1	$Trinity R.	1.000	0	0	0	1.000	0	0	0
M2	$Iron Gate	1.000	0	0	0	1.000	0	0	0
M3	$Trinity (f)	1.000	0	0	0	1.000	0	0	0

APPENDIX A.—*Continued.*

Map code	Population	Locus and alleles									
		Ldh-5			Mdh-1,2			Mdh-3,4			
		100	90	70	100	120	27	100	121	70	83
A1	Babine	1.000	0	0	1.000	0	0	1.000	0	0	0
B1	Tete Jaune	1.000	0	0	1.000	0	0	1.000	0	0	0
B2	Clearwater	1.000	0	0	1.000	0	0	0.989	0.006	0.006	0
B3	Chilco	1.000	0	0	1.000	0	0	0.990	0	0.010	0
B4	Stuart–Nechako	1.000	0	0	1.000	0	0	0.936	0	0.064	0
C1	$Big Qualicum	1.000	0	0	1.000	0	0	1.000	0	0	0
C2	$Puntledge	1.000	0	0	1.000	0	0	0.948	0.037	0.015	0
C3	$Quinsam	0.966	0.034	0	1.000	0	0	0.843	0.103	0.054	0
C4	$San Juan	1.000	0	0	1.000	0	0	0.990	0.010	0	0
C5	$Capilano	0.995	0.005	0	1.000	0	0	1.000	0	0	0
C6	Nooksack SF	1.000	0	0	1.000	0	0	0.965	0.030	0.005	0
C7	Nooksack NF	1.000	0	0	1.000	0	0	0.965	0	0.035	0
D1	$Robertson Ck.	1.000	0	0	1.000	0	0	0.993	0.008	0	0
E1	$Wells Dam	0.980	0.020	0	1.000	0	0	0.970	0.010	0.020	0
E2	$Carson–$Leavenworth	1.000	0	0	1.000	0	0	0.978	0.022	0	0
E3	$Winthrop	1.000	0	0	1.000	0	0	0.990	0.010	0	0
E4	$Priest Rapids	0.964	0.015	0.020	1.000	0	0	0.955	0.030	0.015	0
F1	$Soleduck (sum)	1.000	0	0	1.000	0	0	0.963	0.003	0.035	0
F2	$Soleduck (spr)	1.000	0	0	1.000	0	0	0.975	0.015	0.010	0
F3	$Naselle	1.000	0	0	1.000	0	0	0.944	0.040	0.015	0
F4	$Humptulips	1.000	0	0	1.000	0	0	0.985	0.015	0	0
F5	$Quinault	1.000	0	0	1.000	0	0	0.988	0.013	0	0
F6	Queets	1.000	0	0	1.000	0	0	0.963	0.037	0	0
F7	Hoh	1.000	0	0	1.000	0	0	0.993	0.003	0.003	0.003
F8	$Soleduck (f)	1.000	0	0	1.000	0	0	0.985	0.015	0	0
F9	$Elwha	1.000	0	0	1.000	0	0	0.968	0.015	0.017	0
G1	$Skykomish	0.980	0.020	0	1.000	0	0	0.990	0	0.010	0
G2	$Skagit	0.990	0.010	0	1.000	0	0	0.993	0	0.008	0
G3	$Hood Canal	1.000	0	0	1.000	0	0	0.967	0	0.033	0
G4	$Deschutes	1.000	0	0	1.000	0	0	0.992	0	0.008	0
G5	$Green R.–$Sammish	0.990	0.010	0	1.000	0	0	0.991	0.003	0.005	0
H1	$Cowlitz–$Kalama	1.000	0	0	1.000	0	0	0.988	0.013	0	0
H2	$Lewis R. (spr)	0.990	0.010	0	1.000	0	0	0.965	0.035	0	0
H3	$Cowlitz–$Kalama	0.997	0.003	0	1.000	0	0	0.983	0.017	0	0
H4	$Lewis R. (f)	1.000	0	0	1.000	0	0	1.000	0	0	0
H5	$Washougal R.	1.000	0	0	1.000	0	0	0.990	0.010	0	0
H6	$Eagle Ck.–$McKenzie R.	1.000	0	0	1.000	0	0	0.963	0.037	0	0
I1	$Klickitat R.	1.000	0	0	1.000	0	0	0.970	0.030	0	0
I2	$Spring Ck.–$Big Ck.	1.000	0	0	1.000	0	0	0.945	0.055	0	0
I3	$Warm Spr.–$Round Butte	1.000	0	0	0.995	0.005	0	1.000	0	0	0
I4	Deschutes	1.000	0	0	1.000	0	0	0.985	0.010	0.005	0
J1	Ice Harbor	0.995	0.003	0.003	1.000	0	0	0.985	0.005	0.010	0
J2	McCall–Johnson Ck.	0.976	0.024	0	1.000	0	0	0.998	0.002	0	0
J3	$Rapid R.–Valley Ck.	1.000	0	0	1.000	0	0	0.995	0.005	0	0
K1	$Cole R.–Hoot Owl Ck.	0.988	0.012	0	0.989	0	0.011	0.992	0.008	0	0
K2	$Rock Ck.	1.000	0	0	1.000	0	0	0.968	0.030	0.003	0
K3	$Cedar Ck.	0.975	0.025	0	1.000	0	0	0.995	0.005	0	0
K4	$Trask R. (spr)	0.985	0.015	0	1.000	0	0	0.990	0.010	0	0
K5	Chetco	1.000	0	0	0.998	0.003	0	0.955	0.045	0	0
K6	Lobster Ck.	1.000	0	0	1.000	0	0	0.975	0.025	0	0
K7	$Elk R.	1.000	0	0	0.998	0	0.003	0.983	0.017	0	0
K8	Sixes R. estu.	1.000	0	0	0.945	0.027	0.027	0.993	0.008	0	0
K9	Coquille R. estu.	0.996	0.004	0	0.987	0.011	0.002	0.996	0.004	0	0
K10	Siuslaw Bay	0.982	0.018	0	0.997	0.003	0	0.982	0.018	0	0
K11	$Salmon R.	1.000	0	0	1.000	0	0	1.000	0	0	0
K12	$Nestucca R.–$Alsea R.	0.999	0.001	0	0.999	0.001	0	1.000	0	0	0
K13	$Cedar Ck.	1.000	0	0	1.000	0	0	1.000	0	0	0
K14	$Trask R.–Tillamook Bay	1.000	0	0	0.999	0.001	0	0.985	0.015	0	0
K15	Nehalem estu.	1.000	0	0	1.000	0	0	1.000	0	0	0
L1	$Feather R.	1.000	0	0	1.000	0	0	0.945	0.055	0	0
L2	$Coleman–$Nimbus	1.000	0	0	1.000	0	0	0.968	0.032	0	0
L3	$Feather R.–$Mokelumne	1.000	0	0	1.000	0	0	0.977	0.023	0	0
M1	$Trinity R.	1.000	0	0	1.000	0	0	1.000	0	0	0
M2	$Iron Gate	1.000	0	0	1.000	0	0	0.997	0.003	0	0
M3	$Trinity (f)	1.000	0	0	1.000	0	0	1.000	0	0	0

APPENDIX A.—*Continued.*

Map code	Population	Locus and alleles								
		Mpi				Pgm-1,2			Pgk-2	
		100	109	95	113	−100	−70	−84	100	90
A1	Babine	0.730	0.270	0	0	1.000	0	0	0.095	0.905
B1	Tete Jaune	0.689	0.311	0	0	1.000	0	0	0.421	0.579
B2	Clearwater	0.535	0.465	0	0	1.000	0	0	0.178	0.822
B3	Chilco	0.633	0.367	0	0	1.000	0	0	0.194	0.806
B4	Stuart–Nechako	0.592	0.408	0	0	1.000	0	0	0.383	0.617
C1	$Big Qualicum	0.400	0.600	0	0	1.000	0	0	0.292	0.708
C2	$Puntledge	0.690	0.310	0	0	0.980	0.020	0	0.229	0.771
C3	$Quinsam	0.887	0.113	0	0	0.997	0.002	0	0.151	0.849
C4	$San Juan	0.540	0.460	0	0	0.995	0.005	0	0.180	0.820
C5	$Capilano	0.444	0.556	0	0	1.000	0	0	0.479	0.521
C6	Nooksack SF	0.729	0.271	0	0	1.000	0	0	0.521	0.479
C7	Nooksack NF	0.480	0.520	0	0	1.000	0	0	0.277	0.723
D1	$Robertson Ck.	0.595	0.405	0	0	0.997	0.002	0	0.307	0.693
E1	$Wells Dam	0.670	0.330	0	0	1.000	0	0	0.590	0.410
E2	$Carson–$Leavenworth	0.867	0.133	0	0	1.000	0	0	0.105	0.895
E3	$Winthrop	0.702	0.298	0	0	1.000	0	0	0.505	0.495
E4	$Priest Rapids	0.705	0.295	0	0	1.000	0	0	0.643	0.357
F1	$Soleduck (sum)	0.652	0.338	0.010	0	1.000	0	0	0.345	0.655
F2	$Soleduck (spr)	0.630	0.365	0.005	0	1.000	0	0	0.490	0.510
F3	$Naselle	0.709	0.250	0.005	0.036	0.982	0.012	0.005	0.638	0.362
F4	$Humptulips	0.806	0.194	0	0	0.950	0.045	0.005	0.600	0.400
F5	$Quinault	0.613	0.325	0	0.062	0.970	0.023	0.008	0.575	0.425
F6	Queets	0.713	0.279	0	0.008	0.974	0.025	0	0.333	0.667
F7	Hoh	0.610	0.390	0	0	0.947	0.042	0.011	0.484	0.516
F8	$Soleduck (f)	0.810	0.190	0	0	1.000	0	0	0.365	0.635
F9	$Elwha	0.675	0.290	0.035	0	0.985	0.015	0	0.399	0.601
G1	$Skykomish	0.695	0.305	0	0	1.000	0	0	0.495	0.505
G2	$Skagit	0.768	0.232	0	0	1.000	0	0	0.559	0.441
G3	$Hood Canal	0.608	0.392	0	0	1.000	0	0	0.689	0.311
G4	$Deschutes	0.673	0.317	0.010	0	1.000	0	0	0.649	0.351
G5	$Green R.–$Sammish	0.720	0.280	0	0	1.000	0	0	0.663	0.337
H1	$Cowlitz–$Kalama	0.460	0.515	0.025	0	1.000	0	0	0.722	0.278
H2	$Lewis R. (spr)	0.700	0.280	0.020	0	1.000	0	0	0.378	0.622
H3	$Cowlitz–$Kalama	0.467	0.497	0.037	0	0.995	0.005	0	0.810	0.190
H4	$Lewis R. (f)	0.380	0.490	0.130	0	0.990	0.005	0.005	0.816	0.184
H5	$Washougal R.	0.450	0.550	0	0	1.000	0	0	0.750	0.250
H6	$Eagle Ck.–$McKenzie R.	0.458	0.542	0	0	1.000	0	0	0.931	0.069
I1	$Klickitat R.	0.730	0.260	0.010	0	1.000	0	0	0.570	0.430
I2	$Spring Ck.–$Big Ck.	0.596	0.356	0.048	0	1.000	0	0	0.863	0.137
I3	$Warm Spr.–$Round Butte	0.871	0.129	0	0	1.000	0	0	0.356	0.644
I4	Deschutes	0.704	0.296	0	0	1.000	0	0	0.633	0.367
J1	Ice Harbor	0.793	0.207	0	0	1.000	0	0	0.548	0.452
J2	McCall–Johnson Ck.	0.953	0.047	0	0	1.000	0	0	0.062	0.938
J3	$Rapid R.–Valley Ck.	0.910	0.090	0	0	1.000	0	0	0.139	0.861
K1	$Cole R.–Hoot Owl Ck.	0.868	0.132	0	0	0.992	0.008	0	0.470	0.531
K2	$Rock Ck.	0.740	0.260	0	0	1.000	0	0	0.485	0.515
K3	$Cedar Ck.	0.717	0.283	0	0	0.992	0.008	0	0.378	0.622
K4	$Trask R. (spr)	0.710	0.290	0	0	0.962	0.038	0	0.449	0.551
K5	Chetco	0.790	0.210	0	0	0.980	0.020	0	0.388	0.612
K6	Lobster Ck.	0.550	0.450	0	0	1.000	0	0	0.223	0.777
K7	$Elk R.	0.773	0.227	0	0	0.972	0.023	0.005	0.457	0.543
K8	Sixes R. estu.	0.725	0.275	0	0	0.938	0.040	0.023	0.480	0.520
K9	Coquille R. estu.	0.591	0.409	0	0	0.915	0.050	0.035	0.412	0.588
K10	Siuslaw Bay	0.605	0.395	0	0	0.924	0.073	0.003	0.524	0.476
K11	$Salmon R.	0.677	0.323	0	0	0.920	0.067	0.013	0.279	0.721
K12	$Nestucca R.–$Alsea R.	0.639	0.361	0	0	0.944	0.054	0.002	0.466	0.534
K13	$Cedar Ck.	0.735	0.265	0	0	0.903	0.097	0	0.551	0.449
K14	$Trask R.–Tillamook Bay	0.652	0.346	0	0.003	0.918	0.079	0.003	0.432	0.568
K15	Nehalem estu.	0.780	0.220	0	0	0.918	0.067	0.015	0.438	0.563
L1	$Feather R.	0.510	0.490	0	0	1.000	0	0	0.540	0.460
L2	$Coleman–$Nimbus	0.586	0.414	0	0	0.991	0.009	0	0.592	0.408
L3	$Feather R.–$Mokelumne	0.487	0.513	0	0	0.988	0.011	0	0.651	0.349
M1	$Trinity R.	0.980	0.020	0	0	0.985	0.015	0	0.290	0.710
M2	$Iron Gate	0.975	0.025	0	0	0.942	0.058	0	0.146	0.854
M3	$Trinity (f)	0.990	0.010	0	0	0.997	0.002	0	0.350	0.650

APPENDIX A.—*Continued.*

Map code	Population	Locus and alleles						
		Sod-1				Tapep-1		
		−100	−260	580	1260	100	130	45
A1	Babine	0.936	0.064	0	0	0.921	0.079	0
B1	Tete Jaune	0.931	0.056	0.014	0	1.000	0	0
B2	Clearwater	0.933	0.067	0	0	0.967	0.033	0
B3	Chilco	0.888	0.112	0	0	1.000	0	0
B4	Stuart–Nechako	0.865	0.135	0	0	0.991	0.009	0
C1	$Big Qualicum	0.794	0.206	0	0	0.565	0.435	0
C2	$Puntledge	0.931	0.053	0.016	0	0.803	0.197	0
C3	$Quinsam	0.892	0.098	0.010	0	0.839	0.161	0
C4	$San Juan	0.800	0.190	0.010	0	0.890	0.110	0
C5	$Capilano	0.778	0.157	0.066	0	0.617	0.383	0
C6	Nooksack SF	0.660	0.220	0.120	0	0.653	0.347	0
C7	Nooksack NF	0.570	0.340	0.090	0	0.620	0.380	0
D1	$Robertson Ck.	0.805	0.195	0	0	0.855	0.145	0
E1	$Wells Dam	0.540	0.460	0	0	0.640	0.360	0
E2	$Carson–$Leavenworth	0.821	0.179	0	0	0.872	0.128	0
E3	$Winthrop	0.736	0.264	0	0	0.992	0.008	0
E4	$Priest Rapids	0.550	0.450	0	0	0.793	0.207	0
F1	$Soleduck (sum)	0.725	0.260	0.015	0	0.712	0.288	0
F2	$Soleduck (spr)	0.621	0.379	0	0	0.755	0.245	0
F3	$Naselle	0.684	0.316	0	0	0.854	0.146	0
F4	$Humptulips	0.670	0.290	0.040	0	0.840	0.160	0
F5	$Quinault	0.784	0.206	0.010	0	0.899	0.101	0
F6	Queets	0.875	0.117	0.008	0	0.944	0.056	0
F7	Hoh	0.905	0.095	0	0	0.935	0.065	0
F8	$Soleduck (f)	0.796	0.204	0	0	0.970	0.030	0
F9	$Elwha	0.640	0.290	0.070	0	0.875	0.125	0
G1	$Skykomish	0.565	0.425	0.010	0	0.690	0.310	0
G2	$Skagit	0.707	0.283	0.010	0	0.495	0.505	0
G3	$Hood Canal	0.624	0.366	0.010	0	0.561	0.439	0
G4	$Deschutes	0.627	0.317	0.056	0	0.507	0.493	0
G5	$Green R.–$Sammish	0.625	0.365	0.010	0	0.483	0.517	0
H1	$Cowlitz–$Kalama	0.679	0.321	0	0	0.930	0.070	0
H2	$Lewis R. (spr)	0.620	0.380	0	0	0.875	0.125	0
H3	$Cowlitz–$Kalama	0.615	0.385	0	0	0.923	0.077	0
H4	$Lewis R. (f)	0.571	0.429	0	0	0.880	0.120	0
H5	$Washougal R.	0.560	0.440	0	0	0.780	0.220	0
H6	$Eagle Ck.–$McKenzie R.	0.782	0.213	0.006	0	0.925	0.075	0
I1	$Klickitat R.	0.690	0.310	0	0	0.950	0.050	0
I2	$Spring Ck.–$Big Ck.	0.530	0.470	0	0	0.777	0.223	0
I3	$Warm Spr.–$Round Butte	0.550	0.450	0	0	0.967	0.033	0
I4	Deschutes	0.735	0.265	0	0	0.939	0.061	0
J1	Ice Harbor	0.705	0.295	0	0	0.918	0.082	0
J2	McCall–Johnson Ck.	0.976	0.024	0	0	0.962	0.038	0
J3	$Rapid R.–Valley Ck.	0.944	0.056	0	0	0.886	0.114	0
K1	$Cole R.–Hoot Owl Ck.	0.776	0.221	0.003	0	0.937	0.063	0
K2	$Rock Ck.	0.665	0.330	0.005	0	0.825	0.175	0
K3	$Cedar Ck.	0.828	0.172	0	0	0.914	0.086	0
K4	$Trask R. (spr)	0.890	0.110	0	0	0.800	0.200	0
K5	Chetco	0.800	0.200	0	0	0.840	0.160	0
K6	Lobster Ck.	0.590	0.410	0	0	0.938	0.063	0
K7	$Elk R.	0.655	0.345	0	0	0.920	0.080	0
K8	Sixes R. estu.	0.780	0.220	0	0	0.900	0.100	0
K9	Coquille R. estu.	0.787	0.213	0	0	0.920	0.080	0
K10	Siuslaw Bay	0.841	0.152	0.006	0	0.866	0.134	0
K11	$Salmon R.	0.742	0.258	0	0	0.783	0.217	0
K12	$Nestucca R.–$Alsea R.	0.819	0.181	0	0	0.905	0.095	0
K13	$Cedar Ck.	0.840	0.160	0	0	0.915	0.085	0
K14	$Trask R.–Tillamook Bay	0.895	0.105	0	0	0.881	0.119	0
K15	Nehalem estu.	0.819	0.181	0	0	0.772	0.228	0
L1	$Feather R.	0.620	0.380	0	0	0.950	0.050	0
L2	$Coleman–$Nimbus	0.728	0.267	0.005	0	0.842	0.156	0.002
L3	$Feather R.–$Mokelumne	0.749	0.251	0	0	0.889	0.111	0
M1	$Trinity R.	0.980	0.020	0	0	1.000	0	0
M2	$Iron Gate	0.990	0.010	0	0	0.949	0.051	0
M3	$Trinity (f)	0.895	0.050	0.035	0.020	1.000	0	0

APPENDIX A.—*Continued.*

Map code	Population	Heterozygosity	Dendrogram cluster	Population unit
A1	Babine	0.057	5A	1
B1	Tete Jaune	0.061	5A	1
B2	Clearwater	0.082	5A	1
B3	Chilco	0.071	5A	1
B4	Stuart–Nechako	0.090	5A	1
C1	$Big Qualicum	0.099	6	2
C2	$Puntledge	0.101	3	2
C3	$Quinsam	0.095	3	2
C4	$San Juan	0.074	5A	2
C5	$Capilano	0.118	6	2
C6	Nooksack SF	0.122	8E	3
C7	Nooksack NF	0.124	6	2
D1	$Robertson Ck.	0.105	4	4
E1	$Wells Dam	0.127	8E	6
E2	$Carson–$Leavenworth	0.067	5B	6
E3	$Winthrop	0.076	8C	6
E4	$Priest Rapids	0.118	8E	6
F1	$Soleduck (sum)	0.141	4	4
F2	$Soleduck (spr)	0.097	8E	4
F3	$Naselle	0.114	8B	4
F4	$Humptulips	0.112	8B	4
F5	$Quinault	0.119	4	4
F6	Queets	0.111	4	4
F7	Hoh	0.109	4	4
F8	$Soleduck (f)	0.098	4	4
F9	$Elwha	0.125	8B	4
G1	$Skykomish	0.114	8E	3
G2	$Skagit	0.101	8D	3
G3	$Hood Canal	0.122	8D	3
G4	$Deschutes	0.128	8D	3
G5	$Green R.–$Sammish	0.105	8D	3
H1	$Cowlitz–$Kalama	0.110	2	5
H2	$Lewis R. (spr)	0.113	8C	6
H3	$Cowlitz–$Kalama	0.103	2	5
H4	$Lewis R. (f)	0.113	2	5
H5	$Washougal R.	0.112	2	5
H6	$Eagle Ck.–$McKenzie R.	0.102	1	5
I1	$Klickitat R.	0.099	8C	6
I2	$Spring Ck.–$Big Ck.	0.093	2	5
I3	$Warm Spr.–$Round Butte	0.072	8A	6
I4	Deschutes	0.086	8C	6
J1	Ice Harbor	0.090	8B	6
J2	McCall–Johnson Ck.	0.035	5B	7
J3	$Rapid R.–Valley Ck.	0.045	5B	7
K1	$Cole R.–Hoot Owl Ck.	0.090	8B	4
K2	$Rock Ck.	0.112	8B	4
K3	$Cedar Ck.	0.111	4	4
K4	$Trask R. (spr)	0.124	4	4
K5	Chetco	0.100	8B	4
K6	Lobster Ck.	0.092	5A	4
K7	$Elk R.	0.130	4	4
K8	Sixes R. estu.	0.137	4	4
K9	Coquille R. estu.	0.134	4	4
K10	Siuslaw Bay	0.135	4	4
K11	$Salmon R.	0.128	4	4
K12	$Nestucca R.–$Alsea R.	0.125	4	4
K13	$Cedar Ck.	0.143	4	4
K14	$Trask R.–Tillamook Bay	0.132	4	4
K15	Nehalem estu.	0.131	4	4
L1	$Feather R.	0.124	7	9
L2	$Coleman–$Nimbus	0.123	7	9
L3	$Feather R.–$Mokelumne	0.119	7	9
M1	$Trinity R.	0.032	5B	8
M2	$Iron Gate	0.027	5B	8
M3	$Trinity (f)	0.027	5B	8

APPENDIX B

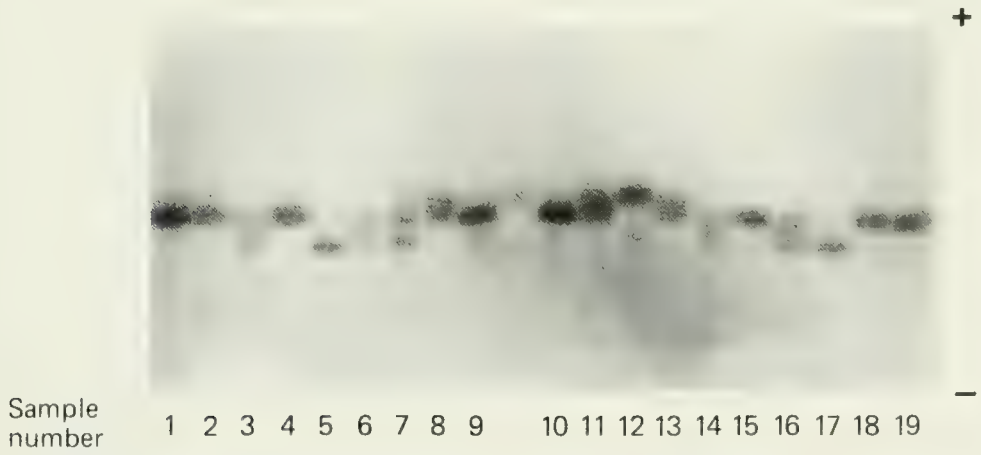
Previously Unreported Genetic Variants

Glutathione reductase (Gr) was the more readily interpreted of the two previously undescribed polymorphic enzymes observed for chinook salmon in this study. The phenotypic forms (App. Fig. 1) were those expected from a dimeric enzyme with three alleles and were consistent with known allelic variants of Gr observed in other vertebrates (e.g., man) (Harris and Hopkinson 1976). The assumption that this variation was a three-allele polymorphism was supported by the conformance of phenotypic ratios to those expected under Hardy-Weinberg equilibrium, the absolute repeatability of expression from independent extractions, and the parallel expression of different tissues (eye and skeletal muscle) from individuals expressing a given phenotype.

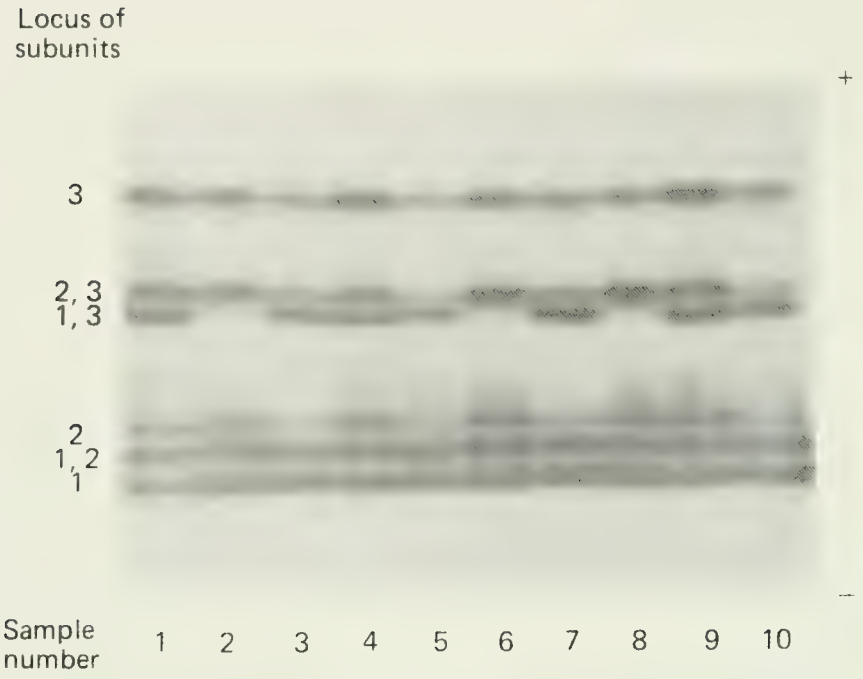
The previously undescribed glucose-6-phosphate isomerase (Gpi) variation was less readily explained. Individuals homozygous for the common alleles at each of the three Gpi loci express a six-banded phenotype that is directly interpreted as having three homodimeric and three heterodimeric bands (App. Fig. 2). An extension of this interpretation also explains additional numbers of bands which arise from allelic forms having different mobilities, or fewer bands resulting from either allelic forms of different loci having common mobilities or from null alleles. However, none of these explanations adequately describe the five-banded Gpi phenotypes that have been found with regularity in some collections.

One explanation that is consistent with the observed phenotypes is that the subunits encoded by a locus aggregate randomly, but that the aggregations for some interlocus combinations are precluded. Such inhibited combinations are common among duplicated loci of salmonids. For instance, subunits of Ldh-3 and Ldh-5 randomly aggregate, as do those of Ldh-3 and Ldh-4; however, Ldh-4 and Ldh-5 subunits do not aggregate (Wright et al. 1975). Mutations precluding aggregation (but not necessarily affecting electrophoretic mobility) must have arisen at some time between the duplication event and the present, and such mutations must have been polymorphic between their arising and their fixation (see Allendorf and Thorgaard 1984, for a review of gene duplication in salmonids).

The above model was tested when gametes and tissues were obtained from individuals of the Priest Rapids stock where five-banded Gpi phenotypes were commonly observed. Because of difficulty in unambiguously discerning common and presumed heterozygous phenotypes, the only informative crosses were those involving the single parent having a five-banded phenotype. The phenotypic ratios of the two matings involving this individual (App. Table 1) conform to those expected from a Men-



APPENDIX FIGURE 1.—Glutathione reductase phenotypes of chinook salmon from eye fluid extracts. Genotypes include 100/100 (samples 1, 2, 4, 9, 10, 15, 18, 19), 100/85 (samples 3, 6, 14, 16), 85/85 (samples 5, 17), 85/110 (sample 7), 110/100 (samples 8, 11, 13), 110/110 (sample 12).



APPENDIX FIGURE 2.—*Gpi-1(H)* variation in chinook salmon from extracts of skeletal muscle. Samples 2, 6, and 8 are H/H homozygotes. Genotypes of other samples are unknown for the *Gpi-1(H)* allele.

APPENDIX TABLE 1.—Observed and (in parentheses) expected numbers of chinook salmon progeny from parents of known Gpi-1 phenotype assuming Mendelian inheritance of subunits having differential heterodimer forming capabilities. Phenotypic designations are based on Figure 3.

Parental		Observed and (in parentheses) expected number of progeny for genotypes	
Phenotype male	Genotype female	100/100 or 100/H	H/H
H/H	?	41	46
	H/100	(43.5)	(43.5)
	100/100	(87)	(0)
H/H	?	139	0
	100/100	(139.0)	(0)
	H/100	(69.5)	(69.5)

delian variant affecting heterodimer formation between Gpi-1 and Gpi-3 subunits. We therefore conclude that individuals with such five-banded phenotypes are homozygous for an allele at the Gpi-1 or Gpi-3 loci that affects dimer formation between subunits of these loci. The present data give no information regarding which locus encodes the mutant subunit. However, the polymorphism has been recorded and analyzed as a third allele at the Gpi-1 locus [*Gpi-1(H)*] because of the low frequency of mobility variants at this locus, none of which occurred in populations where the allele affecting heteromeric combinations was observed. The correct locus could probably be identified through induced gynogenesis of eggs from females heterozygous for mobility variants at Gpi-1 and Gpi-3, and *Gpi-1(H)* heterozygotes. The gene-centromere distance for *Gpi-1(H)* would match that of the mobility variant of the appropriate locus assuming that gene-centromere distances differ for the loci encoding the mobility variants (e.g., see Thorgaard et al. 1983).

Because of the difficulty in distinguishing the common and the *Gpi-1(H)* heterozygous phenotypes the recorded allele frequencies are based on the square root of the *Gpi-1(H)* homozygous (i.e., five-banded) phenotypes under the assumption that the samples where these phenotypes are observed are in Hardy-Weinberg equilibrium. This assumption is supported by the preponderance of genotypic frequencies in Hardy-Weinberg equilibrium at other polymorphic loci. This restriction results in an inevitable underestimation of the frequency of this allele when its frequency is too low for homozygous expression at reasonable sample sizes.

THE USE OF STATOLITH MICROSTRUCTURES TO ANALYZE LIFE-HISTORY EVENTS IN THE SMALL TROPICAL CEPHALOPOD *IDIOSEPIUS PYGMAEUS*

GEORGE DAVID JACKSON[1]

ABSTRACT

Populations of the sepioid *Idiosepius pygmaeus* were located in mangrove and estuarine localities in the Townsville region of North Queensland Australia in 1986. This species was small, easy to observe and collect in the field and sexually dimorphic, with females being much larger than males.

Statolith microstructures of *I. pygmaeus* proved to be a useful ageing tool which can be used to interpret life history phenomena in this species. Increments were calibrated by marking statoliths in situ with tetracycline and counting the rings laid down subsequent to marking. This validated the daily periodicity of the observed rings.

Statolith discontinuities (checks) were occasionally seen within the microstructures of some specimens. These discontinuities appear to parallel similar structures found in fish otoliths.

Based on statolith analysis, *I. pygmaeus* matured at an age of 1½–2 months. Females were larger and grew faster than their male counterparts. Females of similar age were found to vary considerably in size. The estimates of growth rates and longevity for *I. pygmaeus* suggested multiple generations within one year.

Pannella (1971) discovered daily growth increments within the otolith microstructure. Subsequently a plethora of information has been obtained from otolith microstructural analysis, which has greatly aided studies of fish biology and population dynamics (see Campana and Neilson 1985 for a review of the relevant literature). Growth ring analysis has provided a means to evaluate age structures and growth rates in young fishes, and constitutes a powerful tool for population analysis. Similar growth increments have been observed within the statolith microstructure of many cephalopod species (Clarke 1966; Hurley and Beck 1979; Spratt 1979; Lipinski 1981; Kristensen 1980; Rosenberg et al. 1981; Radtke 1983; Natsukari et al. 1988) although concentric rings do not appear to be laid down in octopus statoliths (Boyle 1983). Radtke (1983) suggested that squid statoliths are analogous to fish otoliths; continuing research is supporting his view.

The majority of cephalopod species appear to be short lived and exhibit rapid growth rates (Packard 1972; Saville 1987). The ability to age cephalopods is critical to understanding life history phenomena and population dynamics. Despite the presence of statolith microstructures, there have been few attempts to use this information to develop a picture of demographic events in the Cephalopoda.

Early in 1986 relatively large populations of the sepioid *I. pygmaeus* were discovered in mangrove/estuarine localities in the Townsville region of North Queensland, Australia. This species was small and markedly sexually dimorphic. *Idiosepius pygmaeus* was readily observed and captured in the field, and it was robust enough to make a useful experimental organism. Moreover its small size suggested a relatively short lifespan, providing the potential of obtaining complete records of age and size specific events.

Microstructural examination of the statolith of *I. pygmaeus* was undertaken. Growth rings were present and could be used as an accurate means of ageing. Most similar studies have focused on Northern Hemisphere temperate squids. This is the first study to analyze statolith ring structure and periodicity in a tropical sepioid.

The research aims of this investigation were twofold: 1) to validate statolith increments as growth rings and 2) to utilize the growth ring data to interpret life history phenomena.

MATERIALS AND METHODS

Idiosepius pygmaeus specimens were captured between May and August 1986, and in May 1987,

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in nearshore mangrove/estuarine localities in the Townsville region which is located in the Central Great Barrier Reef Province. The littoral-dwelling *I. pygmaeus* was easily dipnetted off rocks and along mangrove mud banks in the Ross River and Ross Creek estuaries and in the Townsville marina. Specimens used in morphometric analysis were preserved in 10% formalin buffered with borax, while specimens subsequently used for statolith analysis were frozen.

Measurements were taken with an Olympus SZ binocular microscope[2] equipped with an ocular micrometer eyepiece. All weights are wet weights and were taken by blotting the specimen dry and compressing it to expel any water from the mantle cavity. All lengths measured are dorsal mantle length (DML).

Idiosepius pygmaeus specimens were maintained in aquaria during 1988 using a recirculating seawater system. They were fed ad libitum with the sergestid shrimp, *Acetes sibogae australis*, which were also maintained in the aquaria. The aquaria were kept outside so the specimens would maintain normal diel periodicity.

Sexual maturity was determined by the presence of spermatophores in Needham's sac (i.e., spermatophore sac) in the males and mature oocytes and large nidamental glands in the females.

Statolith Analysis

Idiosepius pygmaeus statoliths are paired calcareous structures situated within the bilobed statocysts which are located at the posterior base of the cephalic cartilage. They were removed by severing the head at the head mantle margin and carefully teasing the statocysts from the skull. The statoliths usually fell free from the anterior wall of the statocysts when the statocysts were pulled apart. Statoliths were placed on a glass slide, washed with water, and dehydrated with 100% ethanol. Final preparation involved flooding the statoliths with xylene and then mounting them anterior (concave) side down in the synthetic mountant and clearing agent, dibutyl-phthalate-polystyrene-xylene (D.P.X.), under a coverslip. This produced adequate clearing in the lateral region of the statolith near the rostrum. The use of D.P.X. provided a high degree of increment resolution obviating the need for grinding techniques.

Mounted statoliths were viewed with an Olympus BH compound microscope (400×). The growth rings observed within the statoliths are distinct bipartite structures consisting of a broad and translucent incremental zone along with a narrower opaque zone. The rings were counted using a drawing tube attached to the microscope to trace lines onto drawing paper. Subsequent counts were then taken from the traced image. To avoid bias, lines were deliberately not counted during tracing. Ring number was ascertained when the same value was achieved with replicate counts. However if there was some variation in replicates, a mean value was taken from at least 3 counts.

The nucleus of the statolith was delineated by a prominent dark ring. This feature has been shown to exist in the statoliths of other species of cephalopods (Hurley and Beck 1979; Kristensen 1980; Rosenberg et al. 1981; Lipinski 1986) and probably represents a hatching mark or first-feeding mark. Specimen age was thus determined as being the number of growth rings from the nucleus to the outer edge of the statolith.

Tetracycline Staining

Specimens used for tetracycline staining were hand-netted in the estuary, maintained in 20 L plastic buckets during collection, transported back to the laboratory and subjected to staining during the same day. Five-hundred mg of tetracycline was dissolved in 2 L of seawater, and the specimens were placed in the solution for 2 hours. A minimum of 2 hours was found to be needed for the tetracycline to be incorporated into the statolith. Tetracycline staining produced a distinct band on the statolith when viewed under ultraviolet irradiation (Leitz Dialux UV compound microscope with kp500 filter and ultra high pressure mercury lamp); the inner edge of the band corresponded to the growth increment deposited during the time of staining. The temporal mark on the statolith was used to calibrate the periodicity of the subsequent rings laid down.

RESULTS

Idiosepius pygmaeus apparently is predominantly a shallow-water estuarine species. No specimens have been captured from benthic sampling on the nearby continental shelf (P. Arnold[3]). Three-hundred

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[3]Peter Arnold, Queensland Museum (North Queensland Branch), Flinders Street, Townsville, Queensland 4810, Australia, pers. commun.

and twenty-two one-half hour oblique Tucker Trawl plankton samples taken at a number of stations across the Central Great Barrier Reef Lagoon (Jackson and Hartwick unpubl. data) yielded only 19 *I. pygmaeus* specimens, even though numerous other cephalopod larvae were captured. In comparison, up to 171 individuals have been dipnetted during one 2 hour collecting trip along 1.72 km of breakwater in the vicinity of Townsville harbor.

Statolith Structure and Microanatomy

The statoliths of *I. pygmaeus* are complex three-dimensional structures. Because of limited depth of field for one plane of focus, some rings near the nucleus are not discernible when photographed (Fig. 1A; classification is after Clarke 1978). Growth rings are most clearly seen in the lateral region near the rostrum. A specimen stained with tetracycline twice, 17 days and 8 days before death, showed considerable statolith growth over a relatively short period of time (Fig. 1B). In many instances a prominent discontinuity (check) within the statolith corresponded to the time of staining. This feature was particularly useful for subsequent ring counts under the light microscope. A tetracycline stained statolith was selected and photographed under both white light, to identify the daily ring structure (Fig. 1C) and UV light to identify the point of staining (Fig. 1D) from which the subsequent daily rings were laid down. Further validation evidence is given for six tetracycline stained specimens in which the statolith ring sequence could be accurately counted (Table 1).

Statolith checks were also observed within the ring sequence of some field-captured *I. pygmaeus* specimens (Fig. 1A, arrow). Statolith checks are considerably more prominent than the other rings due to a greater degree of transparency in the check region producing enhanced visibility under the light microscope. The degree of enhanced visibility often varied between checks.

Sexual Dimorphism and Maturity

This species shows considerable sexual dimorphism, with females achieving a much greater size than males (Fig. 2). The size for all male specimens collected ranged from 5.8 mm to 10.3 mm and 36 mg to 159 mg in weight, while females ranged from 6.5 mm to 17.6 mm and weighed between 67 mg and 655 mg.

The reasons for the marked size-related sexual dimorphism in *I. pygmaeus* could be ascertained by ageing individual males and females. Females achieve a larger size predominantly by growing at a much faster rate than males and to a lesser extent by growing older than males (Fig. 3). Moreover, weight is an unreliable index of age, particularly in females, as individuals of similar ages can vary considerably in weight (Fig. 3).

Males mature as small as 6.8 mm and 62 mg and as young as 42 days. In contrast, females matured at around 13 mm and 400 mg and as young as 60 days. The largest immature female aged was 59 days and was 339 mg and 13.7 mm. All males examined had spermatophores present although the youngest specimen caught (35 days, 6.1 mm, 40 mg) only had one spermatophore in Needham's sac.

Based on statolith age analysis, the lifespan of *I. pygmaeus* is quite short, with the oldest specimens aged being 67 days and 79 days for males and females respectively.

TABLE 1.—Age validation information for *Idiosepius pygmaeus* (L: lateral region; R: rostrum; DD: dorsal dome).

Mantle length (mm)	Sex	Date stained	Date experiment terminated	Number of days	Number of increments	Area of statolith where rings viewed
7.6	M	28 May 1986	3 June 1986	6	6	L
11.1	F	14 March 1988	26 March 1988	12	12	R
7.3	F	22 April 1988	28 April 1988	6	6	L
8.1	M	10 June 1988	13 June 1988	3	3	L
12.9	F	14 March 1988 25 Mach 1988	31 March 1988	10 (between staining)	9	DD
14.4	F	22 April 1988 1 May 1988	9 May 1988	9 (between staining)	9	L

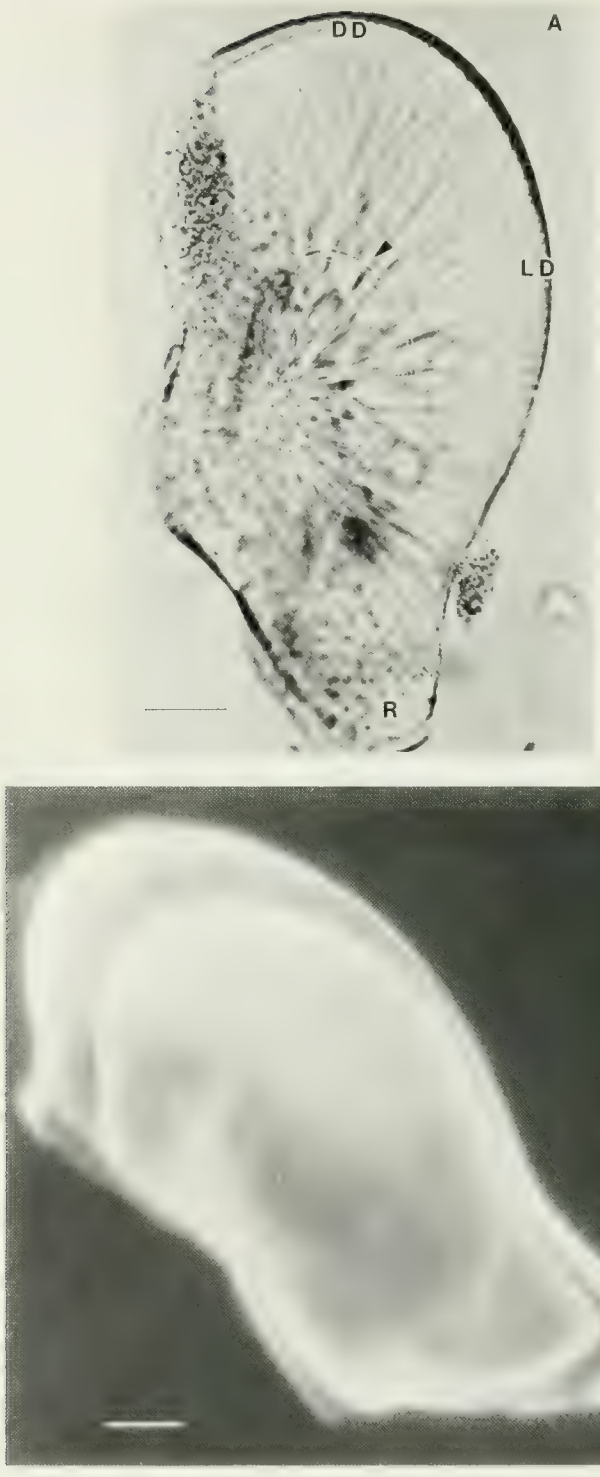

FIGURE 1.—Light micrographs of *Idiosepius pygmaeus* statoliths. A: Whole statolith from male age 36 days, length 7.2 mm, showing complex shape and ring structure, DD = dorsal dome, LD = lateral dome, R = rostrum, arrow indicates prominent check (scale bar = 24 μ); B: Whole statolith stained with tetracycline twice

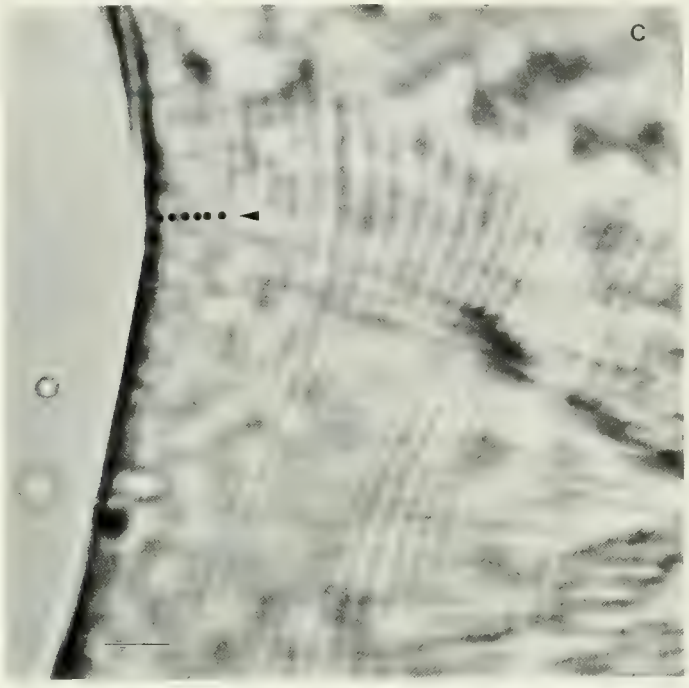

FIGURE 1.—*Continued*—17 days and 8 days before death (viewed under incident UV light) (scale bar = 25 μ); C: Ring sequence from specimens maintained in Aquarium for 6 days poststaining, arrow indicates point of staining (scale bar = 5 μ); D: Same specimen as 1C under UV light to highlight fluroescent band.

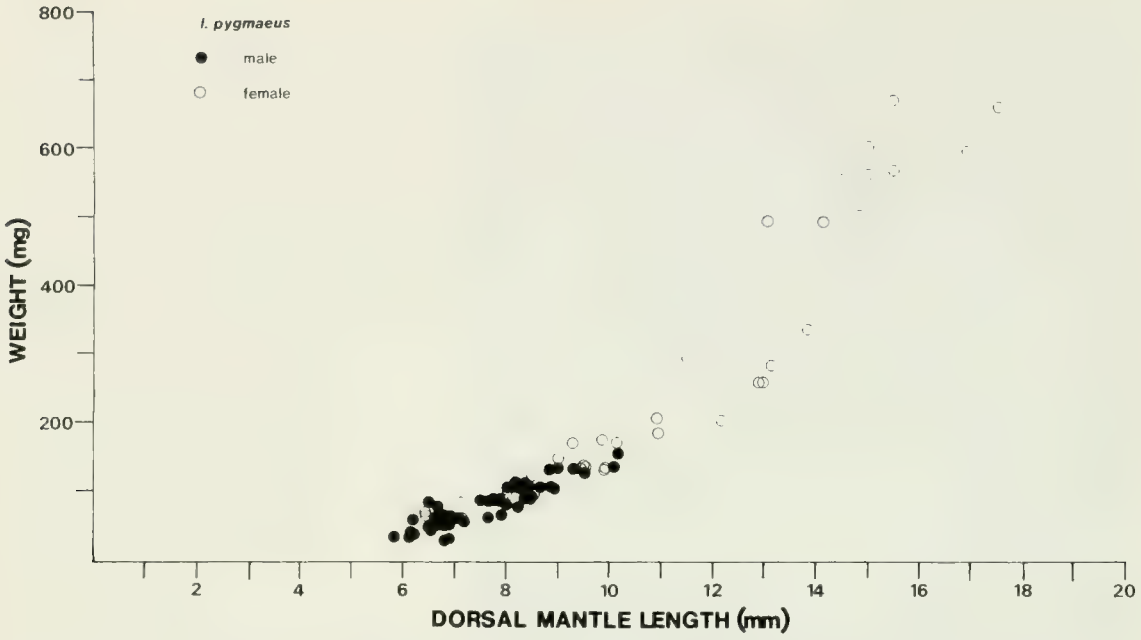

FIGURE 2.—Relationship between weight and dorsal mantle length for male and female *Idiosepius pygmaeus* specimens.

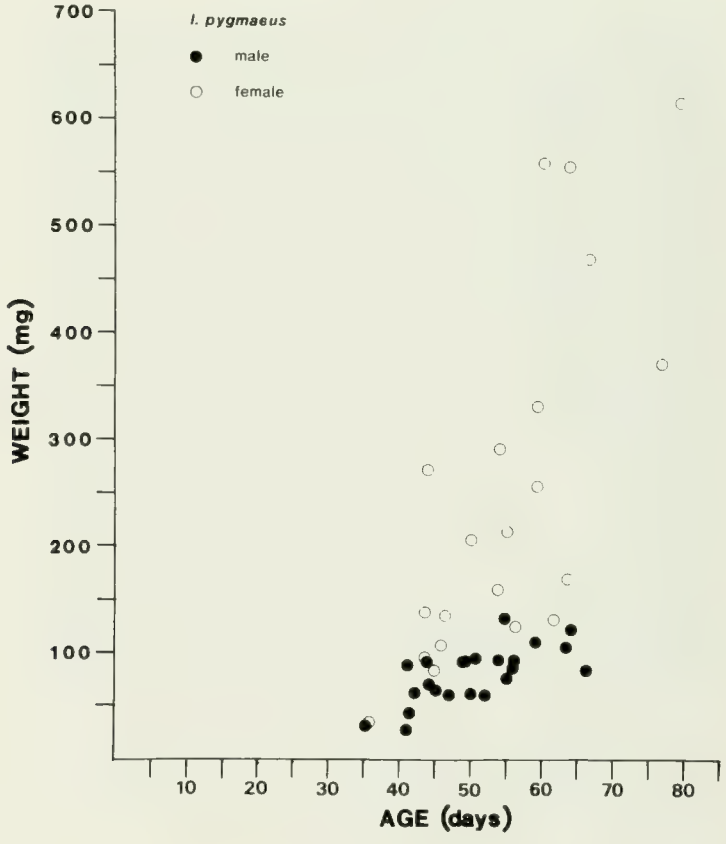

FIGURE 3.—Relationship between age (ring number) and weight for male and female *Idiosepius pygmaeus* specimens.

DISCUSSION

Daily periodicity in ring formation has been shown for both *Illex illecebrosus* (Hurley et al. 1985; Dawe et al. 1985) and *Alloteuthis subulata* (Lipinski 1986) in the North Atlantic, and for juvenile specimens of the pacific market squid, *Loligo opalescens*, (Yang et al. 1986). The tropical *I. pygmaeus* has provided further evidence for the one-ring:one-day hypothesis in a nonteuthoid cephalopod and suggests that daily statolith rings are a widespread phenomenon among cephalopod species.

The fact that the rings were most consistently visible near the lateral dome region of the statolith of *I. pygmaeus* is probably related to the thinness in this region, which allows better light transmission. A similar situation has been found in the dolphin fish *Coryphaena hippurus*. This fish has a complex elongate sagitta. Consequently when mounted in a clearing agent, growth rings are visible only on the otolith's lateral region rather than on the longest axis (Oxenford and Hunte 1983).

Check marks within the microstructure of the statoliths of *I. pygmaeus* are very similar to stress checks observed in fish otoliths (Pannella 1980; Campana 1983; Campana and Neilson 1985). Stress in fish has been shown to reduce branchial uptake of calcium, resulting in a calcium-poor check structure that is visually prominent compared to the surrounding daily increments. The visual intensity of a check in fish is often proportional to the magnitude and duration of the stress that caused it (Campana 1983). The fact that a statolith check was often induced when *I. pygmaeus* was captured and exposed to tetracycline suggests that stress is also a likely cause for statolith check formation. The trauma of capture, confinement in low oxygen conditions during collection along with subsequent staining and temperature shock associated with the transfer to aquaria, all could contribute to inducing a statolith check.

The fact that *I. pygmaeus* matures at an early age, suggests that it is capable of a number of generations in any one year. This agrees with comments by Voss (1983) that small cephalopod species are probably capable of multiple generations per year.

Although size-related sexual dimorphism is common in cephalopods the condition observed in *I. pygmaeus* is unusual and approaches one end of the continuum with the exception of species of pelagic octopods with dwarf males (e.g., *Argonauta* spp.) (Wells and Wells 1977). This study confirms that statolith microstructures provide a means for ageing cephalopods.

ACKNOWLEDGMENTS

I would like to thank R. F. Hartwick who provided valuable assistance throughout this research, J. H. Choat for offering useful suggestions and for critically reading the manuscript, N. E. Milward for advice during the project, C. C. Lu for identification of cephalopod specimens, and C. H. Jackson for assistance with field collecting and preparation of figures.

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DESCRIPTION AND SURFACE DISTRIBUTION OF JUVENILE PERUVIAN JACK MACKEREL, *TRACHURUS MURPHYI*, NICHOLS FROM THE SUBTROPICAL CONVERGENCE ZONE OF THE CENTRAL SOUTH PACIFIC

KEVIN BAILEY[1]

ABSTRACT

Juvenile Peruvian jack mackerel, *Trachurus murphyi*, were collected with a dip net and from albacore stomachs during research cruises to the Subtropical Convergence Zone of the central South Pacific between January and March of 1986 and 1987. The morphometrics and meristics of 40 specimens measuring 46 to 83 mm SL are presented. The predominance of *T. murphyi* in the diet of albacore suggests that the jack mackerel are abundant between latitudes 34°S and 41°S, longitudes 127°W and 165°W during the austral summer. Evidence of the transpacific distribution of *T. murphyi* along the Subtropical Convergence Zone is presented.

Between January and March of 1986 and 1987, research vessels of the New Zealand, United States, and French Governments surveyed the Subtropical Convergence Zone east of New Zealand to determine the extent of the albacore, *Thunnus alalunga*, resource and its potential for exploitation by surface trolling. Stomachs of troll caught albacore were collected to investigate their feeding habits.

A preliminary analysis of stomachs collected during 1986 showed that albacore from the central South Pacific fed almost exclusively on juvenile jack mackerel of the genus *Trachurus*. Although partially digested, the jack mackerel were identifiable as *T. murphyi* Nichols from the descriptions of Berry and Cohen (1974), Kotlyar (1976), and Shaboneyev (1980). This identification was supported by Smith-Vaniz[2] and confirmed with live specimens caught in 1987.

This paper summarizes the morphometrics and meristics of juvenile jack mackerel from the Subtropical Convergence Zone of the central South Pacific, and describes their surface distribution with respect to predation by albacore.

MATERIAL AND METHODS

Jack mackerel were collected from the stomachs and regurgitum of albacore caught during daytime surface trolling by RV *Townsend Cromwell*[3] (cruises TC-86-01 and TC-87-01) and RV *Coriolis*[4] (cruise Prosgermon87), and by dipnetting from schools of jack mackerel attracted to the *Townsend Cromwell*'s lights during the night. Stomach contents were preserved in buffered 10% formalin on *Townsend Cromwell* and frozen on *Coriolis*. In the laboratory the contents were sorted and counted, and their displacement volumes measured. The least digested mackerel were measured to the nearest lower mm of fork length. Where possible the number of scales and scutes along the lateral line and the end point of the accessory lateral line were determined to verify that only one species of *Trachurus* was present (Berry and Cohen 1974).

Live *Trachurus murphyi* were caught with a dip net on two occasions during cruise TC-87-01. These specimens were photographed and preserved in 70% ethanol. On three other occasions, dipnetting was unsuccessful.

Forty jack mackerel (46–83 mm SL) were examined in detail, 1 collected in 1986 and 39 in 1987 (Table 1). Five specimens are catalogued in the National Museum of New Zealand, Wellington (NMNZ 21410) and four in the Academy of Natural Sciences, Philadelphia (ANSP 158517).

[1]Ministry of Agriculture and Fisheries, Fisheries Research Centre, P.O. Box 297, Wellington, New Zealand; present address: South Pacific Commission, Tuna and Billfish Assessment Programme, B.P. D5, Noumea Cedex, New Caledonia.

[2]W. Smith-Vaniz, Academy of Natural Sciences, Philadelphia, PA 19103, pers. commun. August 1986.

[3]U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Ocean Service, Pacific Marine Center, 1801 Fairview Avenue East, Seattle, WA 98102-3767, U.S.A.

[4]Groupement pour La Gestion de Navires Oceanologiques, B.P. 310, 29273 Brest, CEDEX, France.

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Fishery Bulletin, U.S. 87:273-278.

TABLE 1.—Collection data of juvenile *Trachurus murphyi* from the Subtropical Convergence Zone of the central South Pacific by RV *Townsend Cromwell*.

Cruises and date	Time	Position	Sea surface temp (°C)	No.	Size range (SL mm)	Collection method
TC-86-01						
19 Feb.	0700	39°10′S, 146°53′W	17.2	1	56	albacore regurgitum
TC-87-01						
22 Jan.	0500–0545	35°34′–38′S, 149°00′W	19.6	1	46	albacore regurgitum
25 Jan.	0830–1050	37°26′–38′S, 151°27′–37′W	18.8–18.9	4	57–70	albacore regurgitum
27 Jan.	1450	38°37′S, 152°00′W	17.6	2	62	albacore stomach
30 Jan.	1153	37°34′S, 153°11′W	18.8	2	60,66	albacore regurgitum
31 Jan.	0745	37°54′S, 154°48′W	18.7	2	66,72	albacore stomach
	1053	37°48′S, 155°06′W	18.7	1	53	albacore regurgitum
01 Feb.	0500–0535	37°44′S, 156°14′W	19.0	12	59–67	dip net and vessel lights
02 Feb.	0310–0450	39°59′S, 158°00′W	19.2	15	65–83	dip net and submersible light

Morphometric and meristic characters were determined using the procedures described by Hubbs and Lagler (1957), and Berry (1968) with respect to the lateral line. Measurements were made of fork length (FL), standard length (SL), body depth (BD), head length (HL), snout length (SnL), eye diameter (ED) (= orbit length), and pectoral fin length (PL). Additional measurements included the lengths of the curved and straight sections of the lateral line (LL Curv, LL Str), and the height of the largest scale in the curved section (Ht Curv) and the largest scute in the straight section (Ht Str). Measurements were made to the nearest 0.1 mm using vernier calipers and fine-point dividers where practical and a dissecting microscope fitted with an eye piece graticule for SnL, ED, Ht Curv, and Ht Str. Counts were made of dorsal and anal fin softrays, gill rakers on the first gill arch, and scales and scutes along the lateral line. The end points of the dorsal accessory lateral line (LL Acc) and the curved section of the lateral line were measured with reference to the nearest dorsal softray.

DESCRIPTION

The morphometrics and meristics of *Trachurus murphyi* from the central South Pacific are shown in Table 2. The color of live specimens is dark blue dorsally to a line slightly above the lateral midline, and silver-gray immediately below. The fins are clear, with numerous black speckles on the dorsal and caudal fins. In most specimens the operculum has a black spot on the upper posterior margin.

A total of 566 jack mackerel from the two *Townsend Cromwell* cruises, including the 40 specimens described here, was measured. Fork length ranged from 17 to 96 mm (mean FL = 60.7 mm, SD = 12.9 mm). Jack mackerel measured from the 1987 sample (n = 335) differed from the 1986 sample in the occurrence of 31 specimens between 17 and 40 mm length. Although fins appeared completely formed in this size range, specimens below about 35 mm could not be identified beyond genus because scales and scutes did not cover the entire length of the

TABLE 2.—Morphometric and meristic characters of juvenile *Trachurus murphyi* from the Subtropical Convergence Zone of the central South Pacific.

Character[1]	Range	No.	Mean	SD
Measurements (mm)				
FL	52.4–90.3	40	73.4	7.2
SL	46.6–83.1	40	66.4	6.9
	as percent of SL			
BD	19.6–22.5	40	20.6	0.7
HL	26.8–31.9	40	28.6	0.9
SnL	7.6– 9.8	40	8.6	0.4
ED	6.9– 9.4	40	8.0	0.5
PL	18.1–21.8	39	20.3	0.8
LL Curv	31.6–38.6	40	35.3	1.7
LL Str	35.1–41.2	40	37.8	1.2
Ht Curv	3.2– 4.7	40	4.1	0.4
Ht Str	3.9– 5.4	40	4.8	0.4
	as percent of HL			
SnL	28.3–33.8	40	30.2	1.1
ED	25.0–32.1	40	28.0	1.4
Ht Curv	10.0–17.4	40	14.3	1.7
Ht Str	12.2–19.6	40	16.8	1.7
Ht Str/Ht Curv	1.05–1.30	40	1.18	0.07
LL Str/LL Curv	0.95–1.27	40	1.07	0.07
Counts				
Dorsal softrays	30–35	37	33.2	1.4
Anal softrays	26–31	37	28.5	1.2
Scales Curv	48–58	40	52.8	2.5
Scales and scutes Str	43–53	40	48.4	2.8
Scales and scutes total	96–111	40	101.2	3.2
End point LL Acc	1– 5	40	1.9	1.0
End point LL Curv	8–11	40	9.5	0.7
Gill rakers - upper limb	14–18	38	15.5	0.8
- lower limb	40–45	38	41.9	1.5
- total	54–61	38	57.4	1.8

[1]See text page 274 regarding abbreviations

lateral line and the accessory lateral line was not visible. In fish smaller than 25 mm FL the lateral line was not fully developed, but the specimens had the typical shape, pigmentation pattern, and procumbent dorsal spine of *Trachurus* juveniles (Haigh 1972). Jack mackerel collected on *Coriolis* were too digested to measure accurately, but from general body size they were similar to the *Townsend Cromwell* samples.

SURFACE DISTRIBUTION

Trachurus murphyi is a schooling, pelagic species found along the west coast of South America from northern Peru and the Galapagos Islands to southern Chile (Gutierrez 1986). Eggs and larvae have been found over 1,000 km from this coastline (Santander and de Castillo 1971; Gutierrez 1986), and recently two larvae and a juvenile were caught in the Subtropical Convergence Zone at lat. 39°42′S, long. 125°46′W and 40°46′S, long. 139°28′W respectively (Evseenko 1987). In addition, adults have recently been discovered off the east coast of New Zealand, particularly over the Chatham Rise (Kawahara et al. 1988). The surface distribution of juvenile *Trachurus murphyi* shown in Figure 1 was drawn from the positions where they were netted or found in albacore stomachs. The limits of the distribution are from lat. 34°35′S to 42°02′S and long. 127°00′W to 165°00′W. These limits reflect the cruise tracks and fishing effort of *Townsend Cromwell* and *Coriolis*.

Albacore from the *Townsend Cromwell* and *Coriolis* survey areas had similar diets. *Trachurus murphyi* occurred in 93% of the 174 stomachs examined that contained food (66 stomachs from TC-86-01, 72 from TC-87-01, and 36 from Prosgermon87) and comprised 90% of the diet by volume. That albacore fed so heavily on a single prey species in the two areas suggests that *T. murphyi* are relatively abundant and probably present in the unsurveyed area between 140°W and 147°W. Albacore caught to the west of 165°W during the same periods (9 fish from TC-86-01 and 126 from RV *Kaharoa*[5] cruises K03/86 and K04/87) had not fed on *T. murphyi* or other jack mackerel. Unfortunately the number of albacore caught between the easternmost edge of the Chatham Rise (about 175°W) and 165°W was very low and the presence or absence of jack mackerel can not be inferred.

The present study indicates that jack mackerel occur in the area of the Subtropical Convergence Zone encountered by *Townsend Cromwell* (Laurs et al.[6,7]) and in Subtropical Surface Waters to the north. The Subtropical Convergence Zone is characterized by summer surface temperatures of 15° to 18°C (Roberts 1980; Heath 1985); during this study jack mackerel occurred in temperatures of 16.4° to 21.3°C. During cruise TC-87-01 jack mackerel were found in water 0.5° to 3.0°C warmer than in 1986. This may be due to the greater amount of fishing effort in more northern waters in 1987.

DISCUSSION

Body features most often used to separate and identify *Trachurus* species include the number of scales and scutes along the lateral line, the height (or depth) of the largest of these scales and scutes, the endpoint of the accessory lateral line, and the number of gill rakers and dorsal and anal softrays (Berry and Cohen 1974; Shaboneyev and Kotlyar 1979; Stephenson and Robertson 1977). Three species of *Trachurus* are recognized from the South Pacific: *T. declivis* and *T. novaezelandiae* from temperate waters of New Zealand and Australia (Stephenson and Robertson 1977), and *T. murphyi*. The latter can be separated from the former two species by having on average 18 more scales and scutes along the lateral line.

The juvenile *Trachurus murphyi* examined here are identical in most respects with published descriptions of the species (Table 3) and closely resemble the large jack mackerel from New Zealand waters identified as *T. murphyi* by Kawahara et al. (1988). Unfortunately, Evseenko (1987) did not provide a description of his juvenile *T. murphyi* from the central South Pacific.

A noticeable difference with the present specimens is the significantly fewer gill rakers as compared with the descriptions of Shaboneyev and Kotlyar (1979) (Z test, $P < 0.05$) and Berry and Cohen (1974) (Student's t test, $P < 0.05$, df = 48). This difference is probably related to the size of fish examined as Ahlstrom and Ball (1954) found a similar difference in gill raker number between juveniles and adults of the closely related *T. symmetricus*. Other diagnostic features appear com-

[5]Ministry of Agriculture and Fisheries, Fisheries Research Centre, P.O. Box 297, Wellington, New Zealand.

[6]Laurs, R. M., K. A. Bliss, and J. A. Wetherall. 1986. Preliminary results from R/V *Townsend Cromwell* South Pacific albacore research survey. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep LJ-86-13, 80 p.

[7]Laurs, R. M., K. Bliss, J. Wetherall, and B. Nishimoto. 1987. South Pacific albacore fishery exploration conducted by U.S. jig boats during early 1987. Southwest Fish. Cent. La Jolla Lab., Natl. Mar. Fish. Serv., NOAA, Admin. Rep LJ-87-22, 31 p.

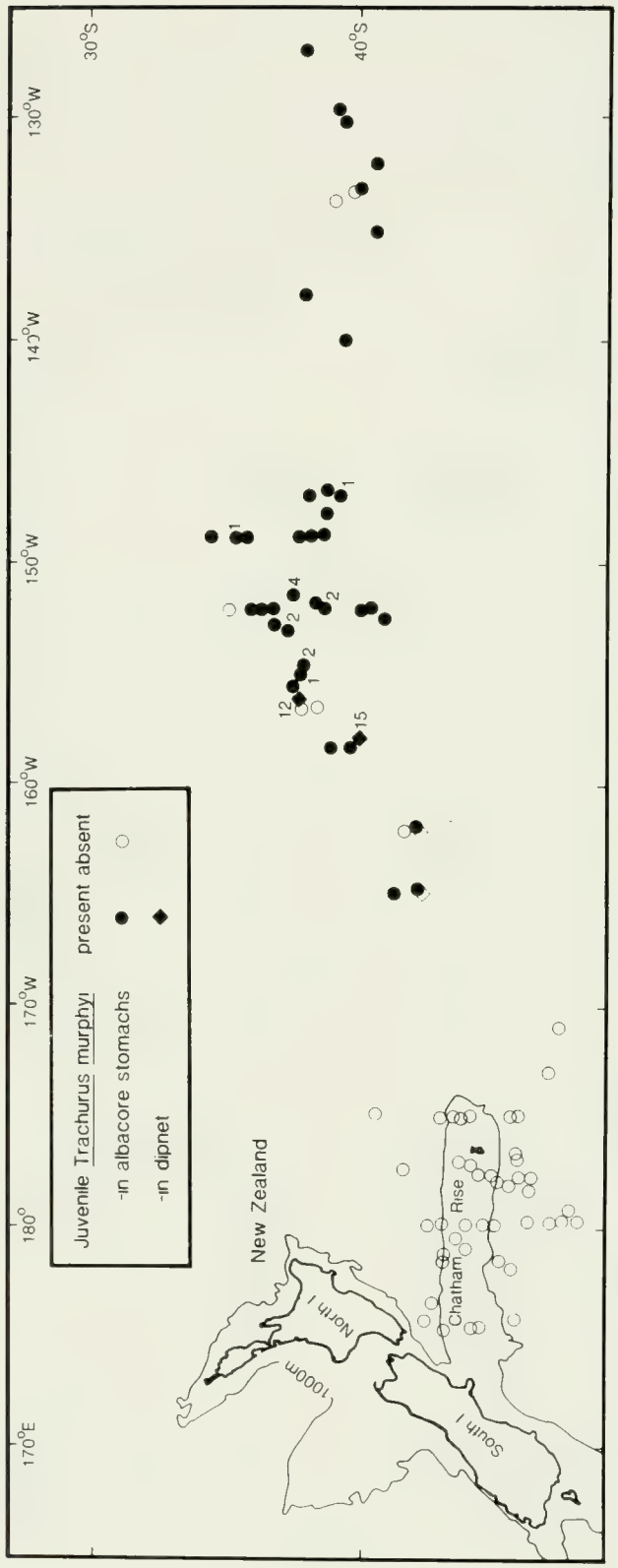

FIGURE 1.—The surface distribution of juvenile *Trachurus murphyi* from the Subtropical Convergence Zone of the central South Pacific, January-March 1986 and 1987. (numbers refer to the 40 specimens examined here)

TABLE 3.—Comparison of meristic and morphometric characters of *Trachurus murphyi* (numbers shown are range and mean).

Distinguishing character[1]	Present study juveniles	Hildebrand (1946) juveniles	Hildebrand (1946) adults	Berry and Cohen (1974) juveniles & adults	Shaboneyev and Kotlyar (1979) adults
Size range (SL mm)	46–83	60–117	485–497	94–552	233–475 (FL)
Number examined	40	—	7	17	250
Scales and scutes					
number Curv	48–58 (52.8)	—	—	51–56 (53.0)	46–55 (50.9)
number Str	43–53 (48.4)	—	—	41–50 (44.8)	44–56 (49.4)
number total	96–111 (101.2)	—	93–104	94–106 (97.8)	92–107 (100.3)
Ht Curv (%SL)	3.2– 4.7 (4.1)	—	—	4.6–5.6	3.1– 5.1 (4.1)
Ht Str (%SL)	3.9– 5.4 (4.8)	—	—	4.8–5.7	4.1– 5.9 (5.3)
Ht Curv (%HL)	10.0–17.4 (14.3)	15.9–17.5	17.0–20.0	—	11.0–18.6 (14.4)
Ht Str (%HL)	12.2–19.6 (16.8)	15.9–21.3	16.1–18.9	—	13.8–21.7 (17.3)
Endpoint LL Acc	1–5 (1.9)	—	—	1–5	[2]2–7 (4.2)
Gill rakers					
upper limb	14–18 (15.5)	—	15–17	15–18 (16.5)	14–23 (17.2)
lower limb	40–45 (41.9)	—	45–48	42–45 (43.9)	39–49 (44.7)
total	54–61 (57.4)	—	—	58–63 (60.4)	57–68 (61.9)
Softrays					
dorsal	30–35 (33.2)	—	30–33	30–36 (33.6)	[2]32–38 (34.0)
anal	26–31 (28.5)	—	25–27	27–31 (28.9)	[2]26–33 (29.5)

[1]See text page 274 regarding abbreviations.
[2]Included in these counts is the first spine of the second dorsal fin and anal fin.

pletely formed in the juveniles, for example, Santander and de Castillo (1971) noted that fin formation was complete in *T. murphyi* of 13 mm SL. In other *Trachurus* species lateral line scales and scutes are well developed by 35 mm (Ahlstrom and Ball 1954; Haigh 1972; Stephenson and Robertson 1977).

There are significant differences in the numbers of scales and scutes along the curved and straight sections of the lateral line between the present specimens and those described by Berry and Cohen (1974) (Student's t test, $P < 0.05$, df = 51), Shaboneyev and Kotlyar (1979) (Z test, $P < 0.05$), and Kotlyar (1976) (Z test, $P < 0.05$). These differences may be due to how the dividing line between the two sections is defined. When the curved and straight sections are combined into single counts along the entire lateral line, the present specimens only differ significantly from those of Berry and Cohen (1974).

Evseenko (1987) suggested that *Trachurus murphyi* has a spawning area centered on the Subtropical Convergence Zone extending from Chile to between 150°W and 160°W. He based his suggestion on an average transport figure for the area, growth data of *T. symmetricus* and the occurrence of one juvenile and two larvae in the central South Pacific. Results from the present study verifies his suggestion in the central South Pacific and, by using a similar approach, extends the probable spawning area westward to include the Chatham Rise.

It is apparent that *Trachurus murphyi* is found and likely to spawn across the South Pacific from New Zealand to Chile. The abundance of juveniles in the Subtropical Convergence Zone between 127°W and 165°W further suggests that a large commercial resource may exist in the central and western parts of the South Pacific.

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ENERGY UTILIZATION IN BAY ANCHOVY, *ANCHOA MITCHILLI*, AND BLACK SEA BASS, *CENTROPRISTIS STRIATA STRIATA*, EGGS AND LARVAE[1]

JOHN W. TUCKER, JR.[2]

ABSTRACT

Bay anchovy, *Anchoa mitchilli*, and black sea bass, *Centropristis striata striata*, both produce abundant, small, planktonic eggs and larvae, but these appear to have contrasting nutritional strategies. Developmental changes and energy utilization in eggs, unfed larvae, and fed larvae of the two species suggest that black sea bass are better able to resist fluctuations in food availability (survive and grow at lower prey densities). Black sea bass have more time to find food and develop feeding skills—47 hours between first feeding and yolk exhaustion vs. 8 hours for bay anchovies. Sea bass feed more efficiently than anchovies. Over the first 96 hours after first feeding, capture success averaged 85% for sea bass and 60% for anchovies. Gross growth efficiency of sea bass (13%) was more than twice that of anchovies (5%). Sea bass may also be more resistant to starvation because their yolk lasts longer (180 hours vs. 80 hours after hatching) and because, during starvation, their metabolism is lower and they lose body calories at a lower rate.

An important determinant of survival of larval fishes is their ability to fulfill nutritional requirements after yolk energy is exhausted. The manner in which energy is used by fish eggs and larvae may indicate adaptability of early stages relative to food composition or abundance. Differences in energy utilization among species might result from different feeding strategies or from adaptation to different feeding conditions (Hunter 1980).

The bay anchovy, *Anchoa mitchilli*, a clupeiform planktivore, is a major food item for predaceous fishes along the U.S. Gulf and Atlantic coasts. Adults are pelagic and live in shallow coastal waters from the Gulf of Maine to Yucatan, Mexico (Hildebrand 1963). In North Carolina, spawning by large schools occurs just after sunset in estuaries and coastal waters from late April to early September and peaks during late June to early August (Kuntz 1914; Hildebrand and Cable 1930; pers. obs.). Eggs (which lack oil globules) and larvae are planktonic and occur in estuaries and bays and just offshore. Spawning might occur over a wide temperature range (Dovel 1971), but larval growth is best in the mid to high twenties (Houde 1974). Early juveniles are abundant in brackish water and also enter fresh water.

The black sea bass, *Centropristis striata striata*, a perciform piscivore generally found offshore, supports important commercial and sport fisheries along the U.S. Atlantic coast. It is distributed over the continental shelf and in bays from Cape Cod, MA to Cape Canaveral, FL and occasionally to the Gulf of Maine or Florida Keys (Miller 1959; Musick and Mercer 1977). Adults are demersal, and south of Cape Hatteras they are found on rough bottom over the inner shelf. Spawning takes place over the inner shelf, mostly in spring or summer, depending on latitude (Musick and Mercer 1977). Off North Carolina, peak spawning is from March to early June. Eggs (with a single oil globule) and larvae are planktonic and occur in shelf waters of 15–51 m depth (Kendall 1972). Juveniles are often found in high salinity estuaries and bays but move into deeper water as they grow.

Several aspects of the feeding ecology of bay anchovy larvae have been investigated, but little is known about black sea bass larvae. Houde and Schekter (1981, 1983) compared growth and energetics of bay anchovy; sea bream, *Archosargus rhomboidalis*; and lined sole, *Achirus lineatus*, larvae. No studies of black sea bass larval ecology have been published, but the southern sea bass, *C. striata melana*, has been reared under experimental mariculture conditions in Florida (Hoff 1970; Roberts et al. 1976; Harpster et al. 1977).

This paper presents information on developmental events and energy utilization for bay anchovy and

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black sea bass from just after fertilization through the eighth day of feeding. Results are used to infer differences in early survival and growth capabilities in nature. Particularly important are differences during the first 96 hours of feeding, which probably arise from adaptations necessary for exploiting different food supplies. Prey densities tend to be lower in the larval black sea bass's habitat (Theilacker and Dorsey 1980).

MATERIALS AND METHODS

The study was conducted with eggs, unfed larvae, and larvae fed for 8 days. The timing of the following developmental events was noted: hatching (H), completion of eye pigmentation (EP), first feeding (FF), yolk exhaustion (EYS), and death of unfed larvae (S). Measurements were made of notochord length (NL), dry weight, % ash, % total carbon, % total nitrogen, % total lipid, energy content, oxygen consumption, feeding efficiency, and feeding rate.

Egg Sources

Bay anchovy eggs usually (40 collections) were obtained 3–5 hours after spawning (before morula stage) by stationary plankton tows in Pivers Island Channel, near Beaufort, NC. For one series of oxygen uptake measurements, eggs and milt were obtained by stripping ripe adult anchovies. Black sea bass eggs were stripped from six females (313–672 g), in which ovulation had been induced by injection of human chorionic gonadotropin, and they were fertilized artificially (Tucker 1984).

Culture Conditions

Physical conditions for rearing experiments approximated those in natural habitats in North Carolina waters during peak spawning. Temperatures were slightly lower than optimal for growth. Bay anchovies were maintained at 24°C and 32‰ with a 14L:10D photoperiod. Black sea bass were maintained at 20°C and 34‰ with a 12L:12D photoperiod. Fluorescent lighting provided 1400 lux at the water surface. Incubation and rearing took place in one to eight (usually six) 10 L black cylindrical fiberglass tanks of filtered seawater. Initial stocking density was 30 or fewer eggs per liter. First-feeding larval density was reduced to fewer than 15/L. Rotifers, *Brachionus plicatilis*, of the same strain investigated by Theilacker and McMaster (1971) were added when larval eye pigmentation was complete, and densities were maintained at about 20/mL. Phytoplankton, *Chlorella* sp. or *Nannochloris* sp., was also added as food for the rotifers. Nutritional quality of starving rotifers diminishes rapidly. Unless well-fed rotifers are added frequently and all of them are eaten quickly, algae must be present in the rearing tanks to maintain their quality. Good rotifer nutrition also ensures that they continue to reproduce, thus maintaining the full size range. Without algae, rotifers not eaten within several hours become empty shells. Without reproduction, a rotifer population tends to consist entirely of large adults.

Measurements and Calculations

The times of eye pigmentation and yolk exhaustion were determined by microscopic examination. Starvation mortality was determined in the 10 L rearing tanks (5 times for each species, 1–3 tanks). In addition, three starvation mortality determinations were made in 2 L dishes using bay anchovy eggs collected on different nights. For each determination, 25 normally developing eggs were placed in each of eight 2 L black glass dishes; dead eggs and larvae were counted and removed periodically, with 100% recovery.

Egg and larval dry weights were determined directly. Daily samples (usually 30 individuals) were taken randomly from the rearing tanks for determination of dry weight. Each group of specimens was rinsed in distilled water and freeze-dried before weighing. Best-fit regression equations were used to predict dry weight at different ages during development. Notochord length of 10–52 specimens was measured at key times during development. Instantaneous, or specific, growth rate was calculated as $g = (\ln W_n - \ln W_0)/T$, in which W_n is the final weight on day n, W_0 is the initial weight on day 0, and T is the interval in days.

I determined energy content of eggs and larvae directly by calorimetry and indirectly by proximate analysis. Eggs and larvae were sampled periodically for ashing, elemental analysis, total lipid assays (black sea bass only), and bomb calorimetry. Ash weights were determined by combustion for 12 hours at 500°C (0.6–2.0 mg subsamples—anchovies: 9 samples, 1 or 2 replicates, 12 determinations; black sea bass: 9 samples, 1 or 2 replicates, 17 determinations). Total carbon and nitrogen contents were determined with a Carlo-Erba[3] model 1106 elemental analyzer (0.5–1.1 mg, usually triplicate, subsam-

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

ples). Total lipid content of five sea bass samples (triplicate subsamples) was estimated by the sulphophosphovanillin technique (Barnes and Blackstock 1973) using a cholesterol standard. Caloric content of 7–10 h old anchovy eggs and 1-4 h old sea bass eggs (5–12 mg subsamples of five samples for each species—anchovies: 1 or 2 replicates, 8 determinations; sea bass: 3 replicates, 15 determinations) was determined by combustion in an oxygen microbomb calorimeter calibrated with benzoic acid.

Caloric content of larvae was estimated using information on the proportions of protein, lipid, carbohydrate, and ash in larvae. Percent protein was calculated as the product of percent nitrogen and 6.025 (Brett and Groves 1979). Because of sample shortages, the following assumptions were made: 1) Black sea bass carbohydrate content was estimated by subtracting % protein, % total lipid, and % ash from 100%. 2) Bay anchovy carbohydrate content was assumed to be the same as that estimated for black sea bass 7 h eggs, 28 h eggs, 150 h unfed larvae, and 249 h fed larvae. 3) Starving anchovy % ash was assumed to be the same as for fed anchovy larvae. 4) Total lipid content for anchovies at four stages was estimated by subtracting % protein, % carbohydrate, and % ash from 100%. The effect of these assumptions on estimated caloric values is minimal because of the small percentages involved; protein is the predominant constituent. The average energy equivalents for heat of combustion were used for conversion of weight to energy: 5,650 cal/g protein, 8,660 cal/g lipid, and 4,100 cal/g carbohydrate (Brett and Groves 1979).

Oxygen uptake was measured with glass capillary differential microrespirometers (Microchemical Specialties Company), calibrated by the potassium ferricyanide-hydrazine sulfate method (Umbreit et al. 1972). The experimental technique was similar to that described by Grunbaum et al. (1955). The experimental and reference flasks each held 0.65 mL of air, a potassium hydroxide saturated filter paper strip for absorption of carbon dioxide, and 0.35 mL of 0.2 μm filtered seawater. Salinity was 32.0‰ for anchovies and 34.3‰ for sea bass. Temperature was maintained at 24.0 ± 0.05°C for anchovies and 20.0 ± 0.05°C for sea bass in a water bath. Fluorescent lighting provided 300 lux. Slight agitation was provided by the flow of water in the bath. One to six eggs or larvae (number decreasing with age) were placed in each experimental flask. The fish were allowed to adjust for 10–60 minutes, depending on age; the index droplet was stable after 10 minutes, but time was increased to allow for initially greater activity of older larvae to subside after confinement. Measurements were made at all times of the day. To ensure that digestion was essentially complete, measurements with fed larvae began more than 2 hours after feeding had ceased. (Digestion time for larger bay anchovy larvae was 1.5 hours; digestion in sea bream up to 100 μg was almost finished by 2.5 hours; Houde and Schekter 1983.) Oxygen consumption was recorded hourly for periods of 3–9 hours (usually 6 hours). The longest that larvae normally would have to go without food is the length of the dark period (10 hours for anchovies and 12 hours for sea bass). Also, when there is light, larvae expect to eat. Therefore, the measurement period for fed larvae was limited to 7 hours. Regression equations relating oxygen uptake to age were fitted. Metabolic energy (energy budget term M) was estimated from oxygen uptake with oxycalorific equivalents 0.00425 cal/μL oxygen for anchovies (24°C) and 0.00431 cal/μL oxygen for sea bass (20°C). Because movement of larvae in the flasks was restricted and feeding larvae normally were much more active (chasing rotifers) than nonfeeding larvae, the resulting total metabolism values were multiplied by the factor two for lighted periods for fed larvae (14 h/d for anchovies and 12 h/d for sea bass). This is the same procedure followed by Houde and Schekter (1983).

Feeding observations were made in the 10 L rearing tanks without handling or otherwise disturbing the larvae. Numbers observed were 160 anchovies, 20 for each day of feeding; 128 sea bass, 5 the day before first feeding, and 10–20 for each day of feeding. Individual larvae were observed for 10 minutes. The number of prestrike flexes, strikes, and successful strikes were recorded and the following ratios were calculated: 1) successful strikes/flexes, 2) successful strikes/total strikes, and 3) strikes/flexes. Successful strikes/total strikes is referred to as capture success. Feeding incidence is the percentage of larvae that captured prey within 10 minutes. Number of rotifers eaten per day was calculated from the mean of observed 10 min feeding rates for each feeding day. Daily ingestion values (energy budget term I) were calculated with the factor 0.000787 cal/rotifer (Theilacker and McMaster 1971). Weight-specific daily ration was calculated using 0.16 μg/rotifer (best available estimate, from Theilacker and McMaster 1971) and predicted larval weights. Energy-specific daily ration was calculated from ingestion estimates and estimates of body energy in calorie per individual. Weight of wild zooplankton provided to first feeding bay anchovies by Houde and Schekter (1983) averaged 0.15 μg/

individual. Detwyler and Houde (1970) found that during the first four feeding days, bay anchovies ate copepod nauplii, copepodites, and adults with daily average widths in the range 50–112 μm. Because they are much easier to catch than copepods, larger rotifers will be eaten. In this study, growth might have been better with a diverse diet, but rotifers were used because their size range is limited and their nutritional quality is relatively well defined.

Energy utilization on a caloric basis was assessed separately for endogenous (eggs, prefeeding and starving larvae) and exogenous (feeding larvae) nutrition. Energy budgets were constructed, based on the equation

$$I = G + M + F\&U$$

in which I is ingestion, G is growth, M is metabolic needs, F is egestion, and U is excretion. For eggs and unfed larvae, both I and F are near zero. Because energy is needed for embryonic growth and metabolism, and some is excreted, the growth term will be negative. The form

$$G = I - M - F\&U$$

may be more appropriate to consider in the context of growth and survival. G in calories was estimated from dry weight and proximate analysis data. I was estimated from feeding rate data. Oxygen uptake data provided M. Egested and excreted calories (F&U) were estimated by difference. With endogenous nutrition, $G = -M - U$, and $U = -G - M$. With exogenous nutrition, $F\&U = I - G - M$. Because F and U were not estimated separately, assimilation ($A = I - F$) is not considered.

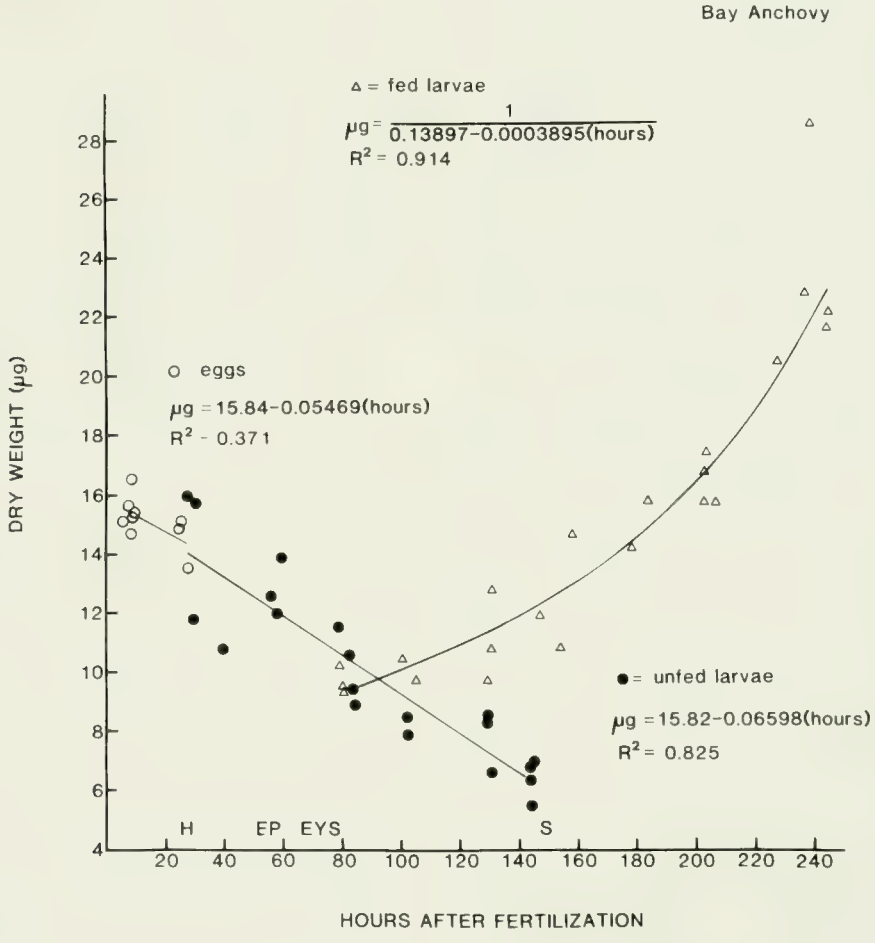

FIGURE 1.—Dry weight of bay anchovy eggs, unfed larvae, and fed larvae.

RESULTS

Developmental Events

Developmental phases were longer for black sea bass at 20°C than for bay anchovies at 24°C (Table 1). Anchovy feeding behavior began within a few hours after EP, and successful feeding was first observed 72 hours after fertilization. Sea bass feeding behavior began several hours after EP, and successful feeding was first observed at 133 hours. Anchovy yolk lasted about 8 hours and sea bass yolk about 47 hours after first feeding. Unfed anchovies in 2 L dishes and 10 L tanks died 5.1 days after hatching (6.2 days after fertilization) and unfed sea bass in 10 L tanks died 8.2 days after hatching (10.2 days after fertilization).

TABLE 1.—Timing of bay anchovy and black sea bass developmental events (hours after fertilization). Starvation = 100% mortality.

	Bay anchovy 24°C	Black sea bass 20°C
Hatching (H)	28	48
Eye pigmentation (EP)	60	110
First-feeding success (FF)	72	133
End of yolk sac (EYS)	80	180
Starvation (S)	150	245

Length and Weight

Throughout development, black sea bass were heavier than bay anchovies of the same age and length, but length at age, and trends in length and weight, were similar. Sea bass egg weight was about twice that of anchovies (32 μg vs. 15 μg; Figs. 1, 2); at hatching, sea bass were heavier (22 μg vs. 14 μg), yet both species were the same length, 2.0–2.1 mm

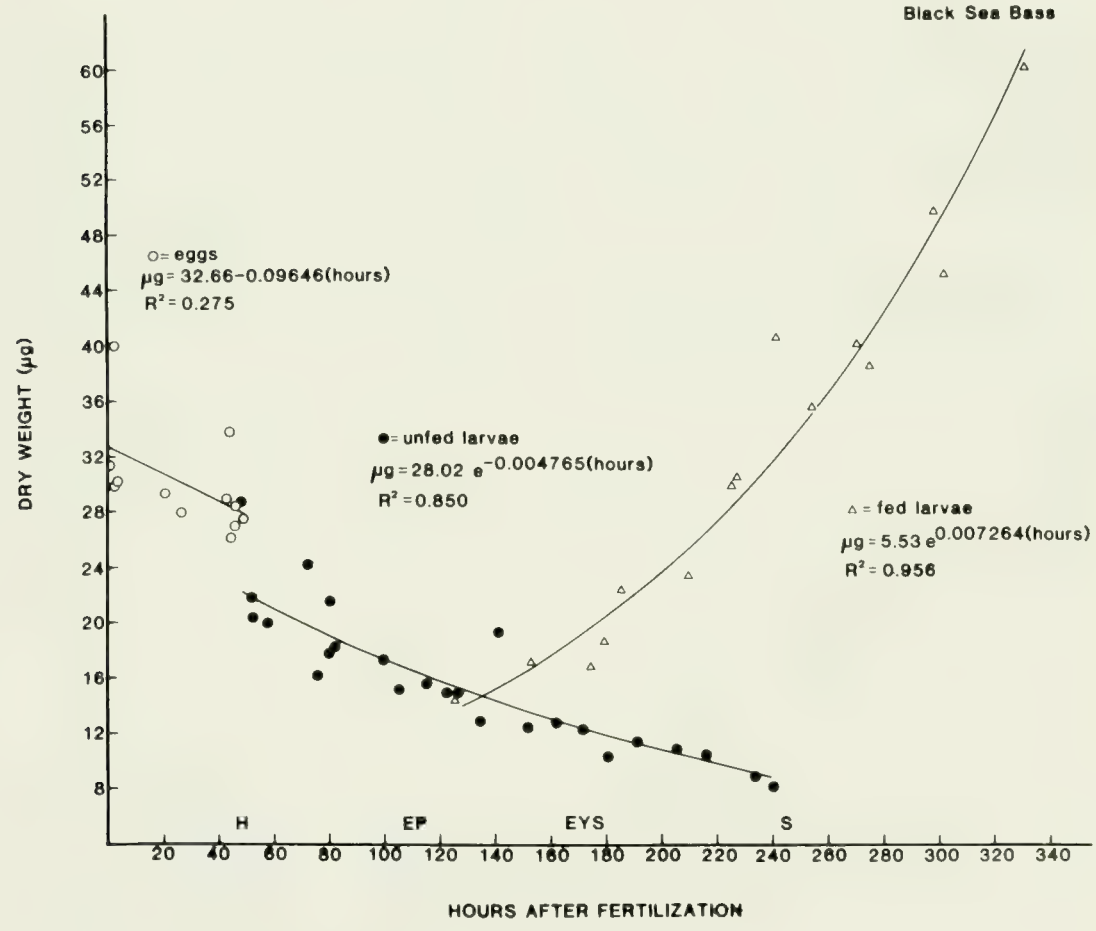

FIGURE 2.—Dry weight of black sea bass eggs, unfed larvae, and fed larvae.

NL. Six days after EYS, fed larvae of both species were 4.1–4.2 mm NL (sea bass 58 μg, anchovies 19 μg). After 168 hours past first feeding, sea bass weighed 49 μg and anchovies 22 μg. Length of unfed larvae reached a maximum between EP and EYS (anchovies, 3.4 mm; sea bass, 3.2 mm) and a minimum between EYS and S (anchovies, 3.0 mm; sea bass, 2.9 mm).

Body Composition

Similar trends in total carbon and total nitrogen content occurred for unfed and fed larvae of both species (Table 2). Percent nitrogen was relatively constant. Percent carbon and C/N decreased between hatching and yolk exhaustion, and then were relatively constant. Although data are limited, there was an apparent decrease in total lipid content of black sea bass throughout development. Values for the five samples were 1 h eggs, 14.5%; 4 h eggs, 15.6%; 217 h unfed larvae, 12.9%; 186 h fed larvae, 12.1%; 298 h fed larvae, 10.4%. Sea bass eggs and larvae contained about 50% more ash than anchovies (Table 3). Bomb calorimetry energy values were similar. Mean values in calories per gram for eggs were anchovies, 5,477 (SD 103, n = 5), ash-free 5,833; sea bass, 5,315 (SD 220, n = 5), ash-free 5,841. Representative calculations of caloric content for energy budgets are shown in Table 4.

TABLE 2.—Carbon and nitrogen content of bay anchovy and black sea bass eggs and larvae during growth and starvation.

Age (h)	Feeding day	n	% Carbon $\bar{x}$	% Carbon SD	% Nitrogen $\bar{x}$	% Nitrogen SD	C/N
Bay anchovy							
Eggs							
8		5	48.9	(0.2)	11.7	(0.1)	4.18
24		2	49.6	(0.1)	12.0	(0.2)	4.12
Unfed larvae							
34		2	49.1	(0.3)	11.2	(0)	4.39
98	2	2	43.4	(0.8)	11.9	(0.1)	3.64
145	4	3	43.1	(0.4)	12.0	(0.2)	3.59
Fed larvae							
92	1	2	43.4	(0.1)	11.6	(0.1)	3.72
146	4	1	44.5		12.2		3.63
202	6	1	42.4		11.9		3.56
248	8	3	43.8	(0.6)	12.0	(0.3)	3.65
Black sea bass							
Eggs							
2		5	46.2	(1.1)	10.7	(0.2)	4.32
45		3	47.7	(0.7)	11.7	(0.2)	4.09
Unfed larvae							
101		1	45.7		11.0		4.14
177	2	2	44.8	(1.3)	12.0	(0.3)	3.74
217	4	1	43.9		11.7		3.75
Fed larvae							
183	3	2	44.6	(0.5)	11.7	(0)	3.82
234	5	2	42.9	(1.6)	11.4	(0.4)	3.78
298	7	1	43.0		11.7		3.68

Oxygen Consumption

The relationship between age and oxygen consumption depended on species, developmental phase, and nutritional status (Figs. 3, 4). In bay anchovies, oxygen uptake increased continuously. In black sea bass, uptake rose until hatching, dropped, then rose again. Uptake decreased for unfed larvae.

Feeding Behavior

Black sea bass capture success was consistently higher than that of bay anchovies (Fig. 5). Anchovy capture success increased from 54% on feeding day 1 to 77% on feeding day 8. Sea bass capture success was 70% on feeding day 1, and during feeding days 2–8 remained relatively constant at 86–94%.

Sea bass feeding incidence was higher than that of anchovies during the first four feeding days (Fig. 5). Anchovy feeding incidence gradually increased from 40% on feeding day 1 to 100% on feeding day 8. Sea bass feeding incidence varied at 85–97% during the first five feeding days and then remained at 100% for feeding days 6–8.

Sea bass larvae had a higher flexing rate but lower strike per flex rate than anchovies. In anchovies, mean number of flexes per hour was 9 at first feed-

TABLE 3.—Ash content of various stages of bay anchovy and black sea bass.

Age (h)	n	Ash (%)	SD (%)
Bay anchovy			
Eggs			
[1]9	5	7.0	0.7
12	4	6.1	0.6
Fed larvae			
85	1	8.7	
146	1	9.0	
248	3	10.1	2.0
Black sea bass			
Eggs			
[1]2	4	9.5	0.7
13	4	9.0	1.9
Unfed larvae			
101	1	11.6	
172	1	13.9	
217	1	14.6	
Fed larvae			
186	1	13.2	
298	1	17.7	

[1]Values from calorimetry for comparison only, not used in energy budget calculations.

ing, 29 on feeding day 2, and 44 on feeding day 8 (feeding day 2–8 mean = 32). In sea bass, mean number of flexes per hour was 48 at first feeding, 74 on feeding day 2, and 59 on feeding day 8 (feeding day 2–8 mean = 63). Anchovy strikes/flexes was 79% at first feeding, 40% on feeding day 2, and 62% on feeding day 8 (feeding day 2–8 mean = 52%). Sea bass strikes/flexes was 38% at first feeding,

TABLE 4.—Calculation of energy content of bay anchovy and black sea bass eggs and larvae. See Table 1 regarding acronyms.

	Bay anchovy					Black sea bass				
	Protein (%)	Lipid[1] (%)	Carboh.[2] (%)	Ash (%)	Energy[3] cal/g	Protein (%)	Lipid (%)	Carboh.[1] (%)	Ash (%)	Energy[3] cal/g
Eggs										
Early	70.5	12.5	10.9	6.1	5,512	64.5	15.0	11.5	9.0	5,415
Late	73.5	12.3	8.1	6.1	5,550	70.5	15.0	5.5	9.0	5,508
Unfed larvae										
Hatchling	67.5	12.3	13.3	6.9	5,424	66.3	15.0	8.4	10.3	5,389
EYS	72.0	9.9	9.5	8.6	5,315	71.7	13.2	1.1	14.0	5,239
Starvation	72.0	15.2	3.8	[4]9.0	5,540	71.7	12.9	0.4	15.0	5,184
Fed larvae										
First feeding	71.8	9.1	10.5	8.6	5,275	67.4	13.3	7.1	12.2	5,251
7 d after FF	71.8	14.6	3.5	10.1	5,465	69.6	10.4	2.1	17.9	4,919

[1]Estimated as the difference between 100% and the other components.
[2]Assumed to be the same as for sea bass at the same age
[3]Including ash
[4]Assumed to be the same as for fed larvae at the same age.

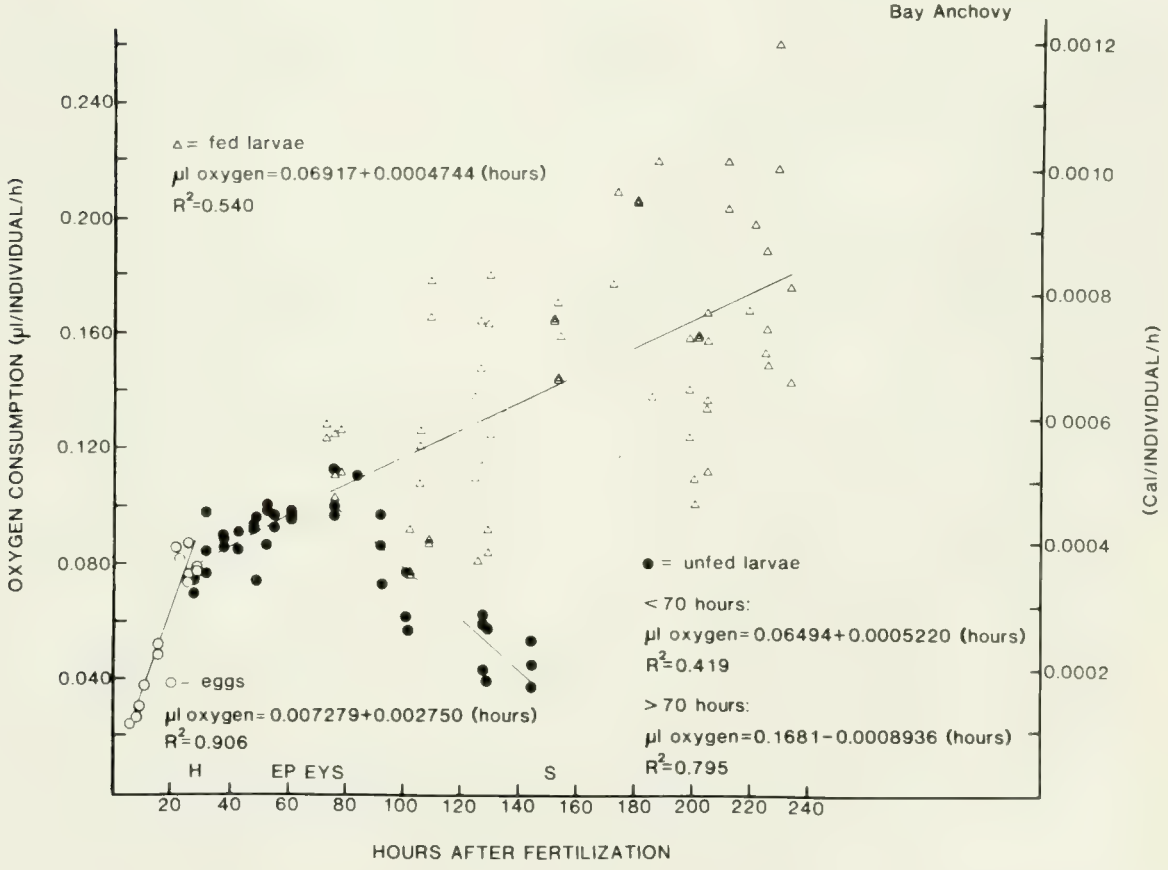

FIGURE 3.—Hourly oxygen consumption by bay anchovy eggs, unfed larvae, and fed larvae.

26% on feeding day 2, and 67% on feeding day 8 (feeding day 2–8 mean = 39%). During the first week of feeding, sea bass inspected more rotifers per unit time than anchovies did, but struck at a lower proportion of them. By the end of the week, these differences had diminished. Although observations were made at all times of the day, no trend with time of day was detected.

Feeding Rate and Daily Ration

Black sea bass feeding rates were considerably higher than those of bay anchovies (Fig. 6). Daily consumption of rotifers by anchovies increased from 4/h during the first feeding day to 13/h on feeding day 8. Sea bass rotifer consumption rose from 11/h on feeding day 1 to 17/h on feeding day 2, dropped

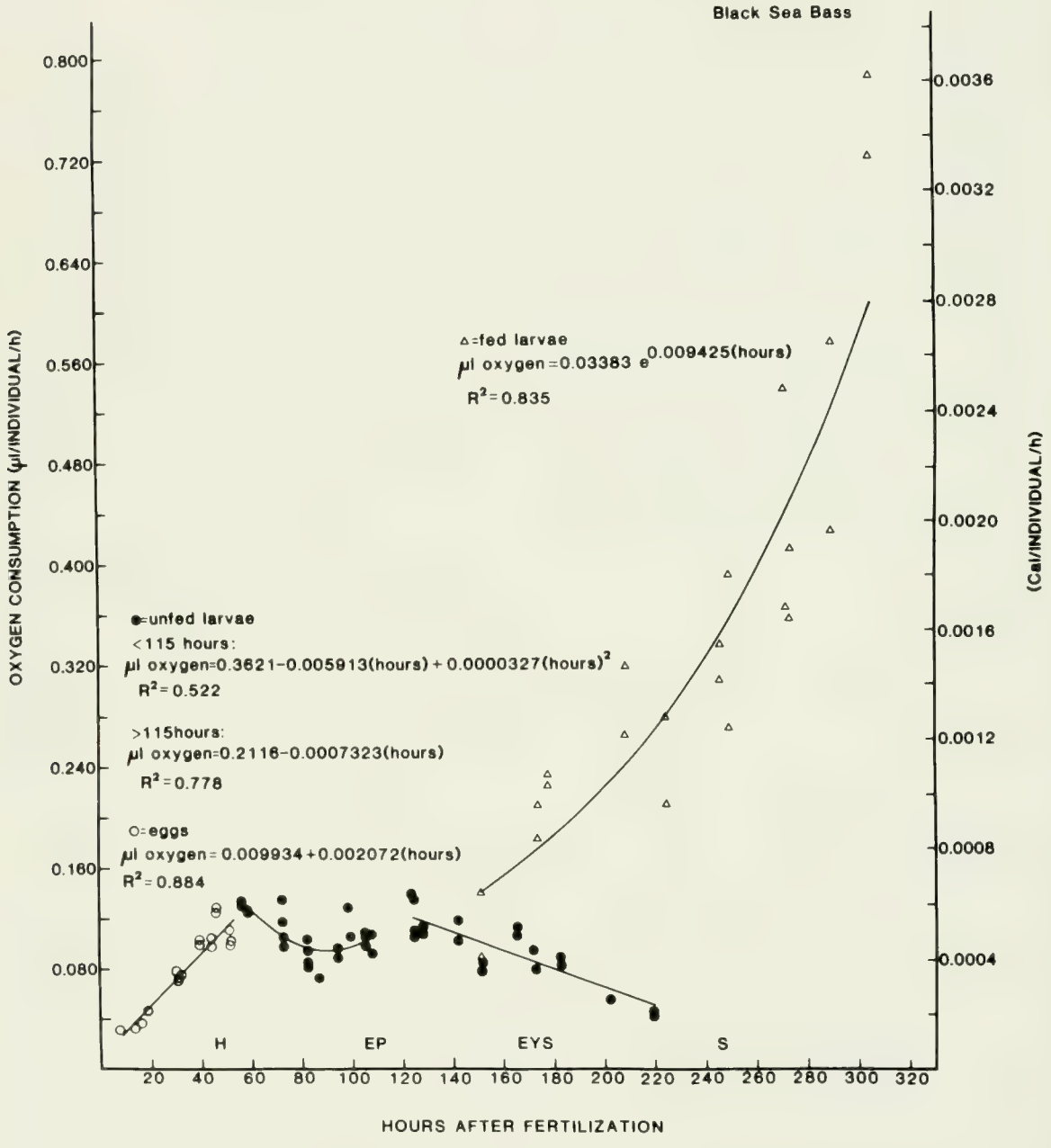

FIGURE 4.—Hourly oxygen consumption by black sea bass eggs, unfed larvae, and fed larvae.

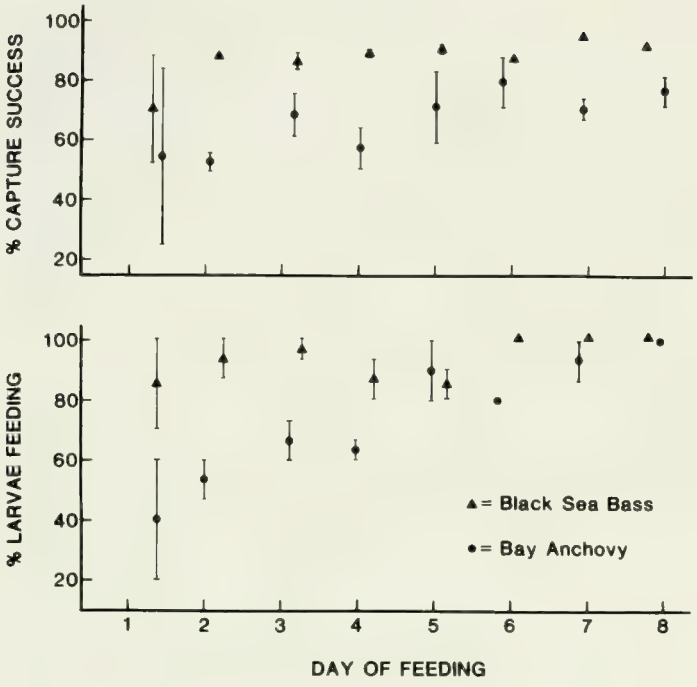

FIGURE 5.—Feeding behavior of bay anchovy and black sea bass larvae (mean ± SE when $n > 1$).

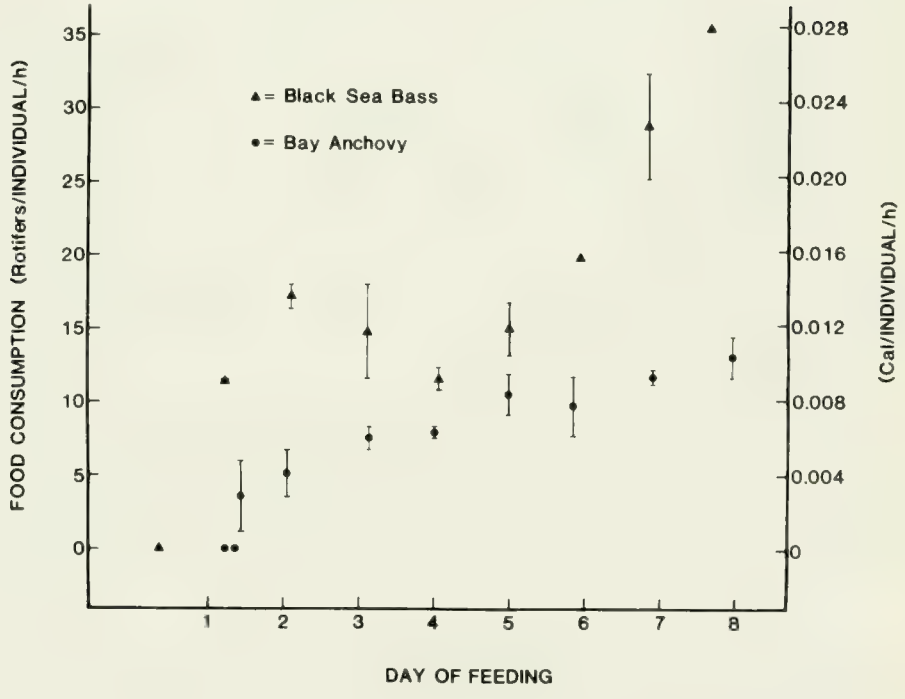

FIGURE 6.—Feeding rates of bay anchovy and black sea bass larvae (mean ± SE when $n > 1$).

to 12/h on feeding day 4, and then rose to 35/h on feeding day 8.

Average daily ration was slightly higher for anchovies than for sea bass. For the 168 hours after first feeding, anchovy daily ration averaged 138% by weight and 126% by calories, compared to 126% by weight and 122% by calories for sea bass.

Energy Budgets

Total energy ingested during the 168 h period was 0.665 cal by bay anchovies and 1.191 cal by black sea bass (Tables 5, 6). Gross growth efficiency (K_1, G/I) and metabolic component (M/I) changed with age of larvae. Anchovy G/I increased from −18% to 15% (overall 9%), while sea bass G/I rose from 9% to 19% then dropped to 12% (overall 14%). Percent of ingested energy used for metabolism by anchovies (M/I) decreased from 44% to 21% (overall 24%), while sea bass M/I increased from 16% to 37% then dropped to 30% (overall 28%). Overall F&U/I was 67% for anchovies and 58% for sea bass.

Four-Day Energy Budgets

A striking difference in early growth capability is revealed by restricting the energy budget to the first 96 hours after first feeding. Black sea bass ingested 1.8 times as much energy as bay anchovies, 0.543 vs. 0.299 cal. Egested and excreted components (F&U/I = 63% and 68%) were similar. Sea bass metabolic component was slightly lower (M/I = 24% vs. 27%) and gross growth efficiency was higher than that of anchovies (G/I = 13% vs. 5%).

DISCUSSION

Length of the interval between first feeding and yolk exhaustion is an important factor affecting survivability of fish larvae because it is the period of transition from endogenous to exogenous feeding. Bay anchovies first feed only 8 hours before their yolk is exhausted, and they do not have positive growth until after EYS. Like Pacific sardines, *Sardinops caerulea* (Lasker 1962), bay anchovies may be particularly vulnerable to food shortages at first feeding. In contrast, black sea bass have 2 days of

TABLE 5.—Energy budget for bay anchovy eggs and larvae during growth and starvation. In the first column, developmental events are indicated in parentheses. G, M, and F&U as percentages of I are given in parentheses.

				G	= I	− M	− F&U
Age (h)	Weight (μg)	Weight change (μg)	Body calories	Growth calories	Food calories	Metabolic calories	Egested and excreted calories
Eggs							
7	15.4		0.085				
28(H)	14.3	−1.1	0.079	−0.006	0	0.003	0.003
Unfed larvae							
33	13.6		0.074		0	0.002	
60(EP)	11.9	−1.7	0.064	−0.010	0	0.010	0
72	11.1	−0.8	0.059	−0.005	0	0.005	0
80(EYS)							
96	9.5	−1.6	0.051	−0.008	0	0.009	−0.001
120	7.9	−1.6	0.043	−0.008	0	0.007	0.001
144	6.3	−1.6	0.035	−0.008	0	0.005	0.003
150(S)	5.9	−0.4	0.033	−0.002	0	0.001	0.001
Fed larvae							
72(FF)	11.1		0.059				
80(EYS)							
96	9.8	−1.3	0.052	−0.007(−18%)	0.039	0.017(44%)	0.029(74%)
120	10.8	1.0	0.058	0.006 (8%)	0.071	0.020(28%)	0.045(64%)
144	12.1	1.3	0.065	0.007 (8%)	0.085	0.021(25%)	0.057(67%)
168	13.6	1.5	0.073	0.008 (8%)	0.104	0.023(22%)	0.073(70%)
192	15.6	2.0	0.084	0.011 (10%)	0.111	0.025(22%)	0.075(68%)
216	18.2	2.6	0.099	0.015 (13%)	0.119	0.027(22%)	0.077(65%)
240	22.0	3.8	0.120	0.021 (15%)	0.136	0.028(21%)	0.087(64%)

Age: from fertilization
Weight: measured
Weight change: from column 2.
Body calories = (weight) (estimated caloric content).
G = Growth calories = change in body calories.
I = Food calories = (average feeding rate) (feeding time) (0.000787 cal/rotifer).
M = Metabolic calories (measured μL O_2/h) (0 00425 cal/μL O_2) (38 hours).
F&U = Egested and excreted calories = I − M − G.

feeding and positive growth before their yolk is exhausted. (Neither species had an advantage in survival time after yolk exhaustion; unfed larvae of both species died within 3 days after EYS.) Starving sea bass weighed 50% more than starving anchovies. Time from hatching to starvation for unfed bay anchovies in both 2 L dishes and 10 L tanks was 122 hours (Table 1). Houde (1974) reported this period to be 126 hours in 35 L aquaria.

Growth of larvae might have been slightly reduced by container size; however, anchovies and sea bass were reared in the same tanks and the comparison should not be affected by container size.

Although growth in length was similar, sea bass gained weight faster than anchovies (Table 7). At hatching, sea bass weighed 1.6 times as much as anchovies. After 7 days of feeding, sea bass weighed 2.2 times as much as anchovies (Figs. 1, 2). At a

TABLE 6.—Energy budget for black sea bass eggs and larvae during growth and starvation. In the first column, developmental events are indicated in parentheses. G, M, and F&U as percentages of I are given in parentheses.

Age (h)	Weight (μg)	Weight change (μg)	Body calories	G = Growth calories	I = Food calories	M = Metabolic calories	F&U = Egested and excreted calories
Eggs							
2	32.5		0.176				
48(H)	28.0	−4.5	0.154	−0.022	0	0.013	0.009
Unfed larvae							
62	20.8		0.112		0	0.008	
86	18.6	−2.2	0.099	−0.013	0	0.010	0.003
110(EP)	16.6	−2.0	0.088	−0.011	0	0.010	0.001
133	14.9	−1.7	0.078	−0.010	0	0.012	−0.002
157	13.3	−1.6	0.070	−0.008	0	0.011	−0.003
180(EYS)							
181	11.8	−1.5	0.062	−0.008	0	0.009	−0.001
205	10.5	−1.3	0.055	−0.007	0	0.007	0
229	9.4	−1.1	0.049	−0.006	0	0.006	0
245(S)	8.7	−0.7	0.045	−0.004	0	0.003	0.001
Fed larvae							
133(FF)	14.9		0.078				
157	17.3	2.4	0.090	0.012 (9%)	0.138	0.022(16%)	0.104(75%)
180(EYS)							
181	20.6	3.3	0.107	0.017(11%)	0.155	0.028(18%)	0.110(71%)
205	24.5	3.9	0.126	0.019(14%)	0.132	0.035(27%)	0.078(59%)
229	29.2	4.7	0.148	0.022(19%)	0.118	0.043(36%)	0.053(45%)
253	34.7	5.5	0.175	0.027(18%)	0.152	0.056(37%)	0.070(45%)
277	41.4	6.7	0.206	0.031(15%)	0.206	0.069(34%)	0.106(51%)
301	49.2	7.8	0.242	0.036(12%)	0.290	0.086(30%)	0.168(58%)

Age: from fertilization.
Weight: measured
Weight change: from column 2.
Body calories = (weight) (estimated caloric content).
G = Growth calories = change in body calories.
I = Food calories = (average feeding rate) (feeding time) (0.000787 cal/rotifer).
M = Metabolic calories (measured μL O_2/h) (0.00431 cal/μL O_2) (36 hours).
F&U = Egested and excreted calories = I − M − G.

TABLE 7.—Percent change in weight and energy content of bay anchovy and black sea bass during developmental phases. Instantaneous growth rates are given. FF = First feeding.

	Hatching to starvation			First feeding to starvation			Hatching to 168 h after FF			First feeding to 168 h after FF		
	Time (d)	Total (%)	Inst. (%)	Time (d)	Total (%)	Inst. (%)	Time (d)	Total (%)	Inst. (%)	Time (d)	Total (%)	Inst. (%)
Bay anchovy												
Weight change	5.1	−58	−17	3.2	−47	−19	8.8	58	5	7.0	98	10
Energy change		−57	−16		−44	−18		58	5		103	10
Black sea bass												
Weight change	8.2	−61	−12	4.7	−42	−11	10.5	120	7	7.0	230	17
Energy change		−63	−12		−42	−12		100	7		210	16

lower temperature (15.5°C), northern anchovies lost 10% of their weight per day during the first 3 days of starvation (Theilacker 1987), versus 17% per day for bay anchovies (Table 5) and 11% per day for black sea bass (Table 6). The greater ash content of sea bass (Table 3) is probably related to their greater size and consequent need for more structural material.

Egg and larval caloric values calculated from proximate analysis data (Table 4) are similar to bomb calorimetry values for anchovy and sea bass eggs and to published values for other species. Calculated values for eggs were 5,512 cal/g for anchovies and 5,415 cal/g for sea bass (less than a 2% difference from measured values, 5,477 and 5,315 cal/g). Energy content of northern anchovy, *Engraulis mordax*, eggs was 5,450 cal/g (Hunter and Leong 1981). Calculated values for larvae fed for 7 days were bay anchovies, 5,465 cal/g, 6,079 cal/g ash-free; black sea bass, 4,919 cal/g, 5,991 cal/g ash-free. These numbers are within the ranges given by Thayer et al. (1973) for postlarvae of four marine fish species: 4,904–6,001 cal/g, 5,694–6,418 cal/g ash-free. Ranges of calculated ash-free values were 5,771–6,088 cal/g for bay anchovies and 5,950–6,099 cal/g for black sea bass. The possible effect of varying lipid and carbohydrate content is small. Houde and Schekter (1983) used a constant value of 5,000 cal/g, and Theilacker (1987) used 5,400 cal/g in constructing energy budgets for larval fish.

Patterns of oxygen consumption were generally similar for the two species (Figs. 3, 4). The decrease for black sea bass during the 0.5 day after hatching probably resulted from reduced activity prior to the development of vision. The interval between hatching and EP was shorter for bay anchovies (1.3 days vs. 2.5 days). Lasker and Theilacker (1962) found that oxygen uptake in Pacific sardines increased just after hatching, but was variable, depending on activity. On the eighth day of feeding, sea bass consumed oxygen at three times the rate of anchovies. At that stage, sea bass had two and a half times as much respiring tissue, and were more active (Q_{O_2} of sea bass was 12 μL O_2/mg/h vs. 9 for anchovies). However, at 20 μg, bay anchovy and black sea bass Q_{O_2} was the same and was intermediate among those of other species (Table 8). Early bay anchovy oxygen uptake was similar to that found by Houde and Schekter (1983), who reported mean uptakes of 0.030 μL/h/egg and

TABLE 8.—Comparison of growth characteristics of well-fed larvae of five species. See Tables 1 and 5 regarding acronyms.

	Northern anchovy[1] 16°C	Bay anchovy[2] 26°C	Bay anchovy[3] 24°C	Black sea bass[3] 20°C	Sea bream[2] 26°C	Lined sole[2] 28°C
Age at FF (d after H)	3.0	~1.5	1.8	3.5	~1.5	~2.0
Capture success at FF (%)	[4]11	49	54	70	53	69
Capture success 20 μg (%)	[4]39	60	74	87	61	81
Daily ration (weight) 17–22 μg (%)	81	281	138	166	198	252
I component 17–22 μg (cal/d)	0.06	0.332	0.136	0.155	0.234	0.297
Oxygen uptake 20 μg (μL O_2/ind/h)	0.134	0.144	0.178	0.179	0.218	0.240
Q_{O_2} 20 μg (μL O_2/mg/h)	6.7	7.2	8.9	8.9	10.9	12.0
M component 17–22 μg (cal/d)	0.010	0.025	0.028	0.028	0.037	0.041
M/I 17–22 μg (%)	17	8	21	18	16	14
Inst. Grth. (wt or cal) 17–22 μg (%)	19	34	19	17	40	32
G component 17–22 μg (cal/d)	0.020	0.041	0.021	0.017	0.050	0.038
$G/I = K_1$ 17–22 μg (%)	33	12	15	11	21	13
$(G+M)/I = CU$ 17–22 μg (%)	50	20	36	29	37	27

[1]Theilacker 1987 (except capture success).
[2]Houde 1974; Houde and Schekter 1980; Houde and Schekter 1983.
[3]Present study.
[4]Hunter 1972.

0.066 μL/h/yolk-sac larva, at 26°C, two degrees higher.

Sea bass were more active, were more efficient feeders, and spent more time feeding than anchovies (Fig. 5). Sea bass also were more capable predators from first feeding through the eighth feeding day. At first feeding, sea bass were 2.5 days older and were better developed than anchovies. Bay anchovies in this study had about the same capture success (Table 8) as bay anchovies and sea bream studied by Houde and Schekter (1980). Black sea bass capture success was similar to that of lined sole. Northern anchovy larvae feeding on 10–60 *Brachionus*/mL at 17°–18°C (Hunter 1972) were less successful than bay anchovies in the present study, but they struck more often and therefore consumed more rotifers per hour. Northern anchovy capture success was relatively low, ranging from 11% at first feeding to 60% on feeding day 8. For 20 μg larvae, a rate of about 50 strikes/h (Hunter and Thomas 1974) multiplied by 39% capture success gives a feeding rate of 20 rotifers/h vs. 13/h for bay anchovies and 16/h for black sea bass.

Daily rations for bay anchovies and black sea bass were intermediate among published estimates from rearing studies using high larval and food densities (Table 8). Theilacker and Dorsey (1980), in a review article, reported weight-specific daily rations of 70–300% for larvae fed one or more prey mer mL. Houde and Schekter (1983) reported high weight or calorie-specific daily rations of 202–379% for 10–100 μg bay anchovies fed 1 copepod nauplius/mL at 26°C.

During the first 3 days of starvation, weight and calorie loss were similar for both species; however, sea bass conserved weight and calories better during the late stages of starvation (Tables 5, 6, 7). Sea bass also gained weight and calories faster when fed (Table 7). Conservation probably resulted partly from a rearing temperature four degrees lower and partly from physiological differences. Better growth probably resulted from a combination of more efficient feeding, higher ingestion rate, lower temperature, and different physiology. During the first 24 hours after EP, fed anchovies lost more weight and calories than unfed anchovies (−0.015 vs. −0.008 cal). During the first 24 hours after EP, fed sea bass lost about the same weight and calories as unfed sea bass (−0.011 vs. −0.010 cal). This implies that anchovies at first lost more energy to feeding activity than they gained from their food, while sea bass broke even.

Overall gross growth efficiencies (G/I) of 9% for anchovies and 14% for sea bass were at the lower end of the known range for early larvae. Published G/I values for larvae fed one or more prey per mL are 11–46% (Theilacker and Dorsey 1980; Houde and Schekter 1983; Theilacker 1987). The decrease in sea bass gross growth efficiency after 4 days of feeding (229 hours, Table 6) may be related to decreasing suitability of rotifers as food for sea bass (Tucker 1984). After the first few days of feeding, larval growth of both species probably would have been enhanced by the addition of larger prey (Hunter 1980). The effect of small prey on growth may have been greater for sea bass, which have larger mouths and probably can handle larger prey. As a larva grows, the benefit:cost ratio for feeding on constant energy food particles tends to decrease (Theilacker and Dorsey 1980). This principle appears to apply to sea bass, as suggested by reduced feeding after the first two days and decreasing growth efficiency after the fourth day. If, in nature, benefit:cost (food energy:expended energy) drops close to one, the rule of fast early growth is violated and the larva is vulnerable to a given type of predator for a longer time.

Overall M/I values of 24% for anchovies and 28% for sea bass were lower than Brett and Groves' (1979) average of 44% for typical, young, well-fed, fast-growing carnivorous fish; however, M/I is likely to be lower in larvae. One explanation for Houde and Schekter's (1983) lower M/I for anchovies (Table 8) is the high ingestion rate. Hunter and Kimbrell (1980) estimated that 3–5 d old Pacific mackerel, *Scomber japonicus*, use about 18% of ingested calories for metabolism at 19°C.

Overall coefficient of utilization (CU), which is metabolizable energy expressed as a fraction of ingested energy, (G + M)/I, was slightly lower in anchovies (33%) than in sea bass (42%). The coefficient of utilization for young fish has been estimated at 73% (G = 29%, M = 44%) by Brett and Groves (1979) and 65–75% by Ware (1975). Ingested energy unaccounted for by growth and metabolism, 67% for anchovies and 58% for sea bass, was assumed to have been egested or excreted, F&U/I. These values are higher than Brett and Groves' (1979) mean of 27% for young fish, but similar to values for other larvae. Larvae are not as efficient at using their food energy as larger fish but do not need as much of it for activity and maintenance.

The energetics approach can be used to compare adaptations to feeding environments. Although rotifers are not normally eaten in large quantities by anchovies or sea bass in nature, the results of this study are probably indicative of normal feeding ecology, especially if larvae encounter patches of food

organisms of similar nutritional value. The bay anchovy larva has low feeding and growth efficiencies, but its food (in estuaries and coastal waters) is relatively abundant. To compensate for low efficiency, it is obligated to feed in high densities of prey. Fluctuations in density of zooplankton prey in estuaries might strongly influence survival and recruitment to anchovy populations. The black sea bass larva feeds and grows more efficiently. It has to because its food (offshore) is not very abundant. The bay anchovy larva seems to be adapted to the high prey densities, and the black sea bass larva to the low prey densities, that characterize their respective habitats (Theilacker and Dorsey 1980). The results of this study parallel those of Houde and Schekter (1983).

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FACTORS INFLUENCING RECAPTURE PATTERNS OF TAGGED PENAEID SHRIMP IN THE WESTERN GULF OF MEXICO

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ABSTRACT

Movements of brown shrimp, *Penaeus aztecus*, and pink shrimp, *P. duorarum*, off the adjacent states of Texas (USA) and Tamaulipas (Mexico) in the western Gulf of Mexico were examined by releasing tagged shrimp within 150 km of each side of the border during May–July 1986. Analysis of recaptures during June–August 1986 indicated that species and release location (state) significantly influenced recapture patterns. Distances travelled prior to recapture, days at large, and movement speeds were greater for shrimp released off Tamaulipas than for shrimp released off Texas. Brown shrimp were recaptured in deeper waters than pink shrimp even though all releases were made at the same depth. Within each species, shrimp released off Tamaulipas were recaptured in deeper waters than shrimp from Texas releases. Relative to shoreline, directional movement of brown shrimp tended to be offshore while that of pink shrimp tended to be alongshore. During the recapture period, fishing effort off Tamaulipas was 13% of that expended off Texas and was expended in deeper waters. Consequently, the fishing mortality was lower off Tamaulipas and tagged shrimp in Tamaulipas waters generally experienced a lower recapture rate, longer times at large, greater distances travelled, and greater depths at recapture. Catch rates off Tamaulipas were also lower than off Texas, even though both fleets used similar fishing gear.

The integration of all components of movement (distance, days at large, direction, recapture depth) was examined by standardizing recaptures north and south of release sites by fishing effort. Paired comparisons of north versus south recaptures per unit effort (R/f) for each of 22 releases indicated no significant differences in brown shrimp movements off Texas or Tamaulipas or in pink shrimp movements off Texas. A significant northward movement of pink shrimp released off Tamaulipas was found.

Brown shrimp, *Penaeus aztecus*, and pink shrimp, *P. duorarum*, are the dominant species caught by commercial shrimp fisheries of the western Gulf of Mexico. Annual landings in the adjoining states of Texas (USA) and Tamaulipas (Mexico) at present average 15,250 t (metric tons) (Klima et al. 1987b; Castro et al. 1986), of which brown shrimp are thought to comprise at least 90% (Slater[3]). In 1981, the United States National Marine Fisheries Service (NMFS) implemented a 45–60 day closure of the Texas shrimp fishery during May–July to increase yield per recruit of brown shrimp (Klima et al. 1982). Mexico has investigated the potential for a similar closure but has not enacted one (Castro y Santiago 1976).

As movement of shrimp out of U.S. waters would reduce the effectiveness of such a closure, shrimp movement patterns were assessed in a general sense by a large-scale, cooperative mark-recapture program in 1978–80 involving NMFS, Texas Parks and Wildlife Department, and Mexico's Instituto Nacional de la Pesca (INP). Tagged brown shrimp and pink shrimp were released between Galveston, TX (lat. 29°15′N, long. 94°45′W) and Tampico, Tamaulipas (lat. 22°15′N, long. 97°50′W) at various depths. Releases were made in estuaries and offshore at various times during March–November 1978–80. Long-distance movements by brown shrimp (up to 620 km) and pink shrimp (up to 428 km), some degree of transborder stock exchange, and a trend for southward movement by both species were found (Castro et al. 1985; Cody and Fuls 1981; Klima et al. 1987a; Sheridan et al. 1987). However, the program did not analyze tag recovery patterns as influenced by fishing effort that is not uniform in time or space.

To assess more precisely the short-term shrimp movements across the U.S.-Mexico border, NMFS and INP conducted a cooperative mark-recapture experiment off southern Texas and northern Tamaulipas during the summer of 1986. The objec-

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tives of this research were to 1) test whether shrimp movement (measured in terms of distance travelled, days at large, speed, direction, or recapture depth) varied according to species, sex, or release location (state), and 2) test for directional movement after recaptures were adjusted by patterns in fishing effort.

MATERIALS AND METHODS

Collection and Tagging of Shrimp

Shrimp were collected by trawl at night off the Texas and Tamaulipas coasts. All collections were made in 16–20 m waters within 5 km of release sites. Shrimp were held in flow-through tanks before and after tagging and until released.

Shrimp were marked with colored, numbered polyethylene streamer tags as described by Marullo et al. (1976). Shrimp between 80 and 140 mm total length were selected because these sizes represented recent recruits. Tagged shrimp were released at 18 m depths within 12 hours of collection using expendable, delayed-release canisters (Emiliani 1971). Each plastic canister was weighted, filled with 50–75 tagged shrimp, sealed with a salt block, and released overboard. The salt block dissolves after 10–15 minutes under water and the canister springs open, releasing the shrimp on the sea floor.

Ten releases of tagged shrimp were made at eight sites between 24°44′N, 97°31′W and 25°57′N, 97°04′W off Tamaulipas (Fig. 1). These releases were made during 30 May–8 June 1986 from the INP ship *BIP-IX*. Twelve releases were made at six sites between 26°05′N, 97°05′W and 26°55′N, 97°17′W off Texas (Fig. 1). The Texas releases were made during 21–28 June 1986 and 7–11 July 1986 from the NOAA ships *Chapman* and *Oregon II*. The order of release sites was randomized given the following restrictions: 1) the 21 June release site was fixed due to vessel cruising speed, and 2) each Texas site was visited once before repeating any site (this was not possible off Tamaulipas). Releases were confined to sites within 150 km of the U.S.-Mexico border (25°57′N) based on shrimp movement speeds that averaged 2.5 km/d during 1978–80 (NMFS, unpubl. data) over a maximum closure of 60 days. In fact, 90% of all transborder recaptures after 1978–80 experiments resulted from releases within 120 km of the border (Sheridan et al. 1987).

No predetermined number of shrimp was set for each night's tagging due to natural variabilities in abundance and catchability. Species composition and size range of released shrimp were estimated by identification and measurement of up to 300 shrimp for each day's release. Identification and measurement of all tagged shrimp was not conducted because such handling could have increased stress and thus influenced behavior or survival of tagged shrimp. Only brown shrimp and pink shrimp were marked and released. Periodic lottery rewards of $50–$500 were offered as incentives to fishermen on both sides of the border to report capture of tagged shrimp with information on location, depth, and date of recapture (Cody and Fuls 1981).

Collection of Recaptures and Fishing Information

Port agents employed by NMFS and INP interviewed fishermen and processors in American and Mexican ports to collect recaptured tagged shrimp and information on fishing locations, landings, and effort. All recaptures during the period 30 May–31 August 1986 were checked for accuracy of date and location and were identified to species when possible. Although recaptures were made after 31 August, only recaptures during the 94 d period were chosen to best reflect summer environments. Recaptures returned with the following inconsistencies were omitted from analyses of movement (although they are included in a general summary of recaptures, Table 1): 1) not identified as brown shrimp or pink shrimp, 2) recapture dates after 31 August 1986, 3) recapture dates prior to or the same as release dates, 4) incomplete latitude and longitude, 5) depth not specified, 6) sex not specified, and 7) recaptured in trawl tows over distances exceeding 9 km. These restrictions reduced the number of usable recaptures from 5,639 (as of the date of last recapture, 5 December 1986) to 3,032 (Table 2).

Port agent interviews of fishermen throughout the U.S. Gulf of Mexico were used to estimate total brown shrimp and pink shrimp fishing effort off Texas during the period 1 June–31 August 1986. These data are collected by specific 9 m depth zones paralleling the coast within quadrangles of one degree latitude and longitude and, as such, are too coarse to examine shrimp movements in detail. Logbooks were voluntarily kept by the captains of 47 Texas shrimp vessels for the duration of the recapture period to collect precise information on starting and stopping points and times, depths, tow durations, and landings. Logbook data were assumed to reflect fishing activities of all vessels off Texas and were used to estimate the amount of total brown shrimp fishing effort (which includes pink shrimp) within 10 minute quadrangles of latitude and longi-

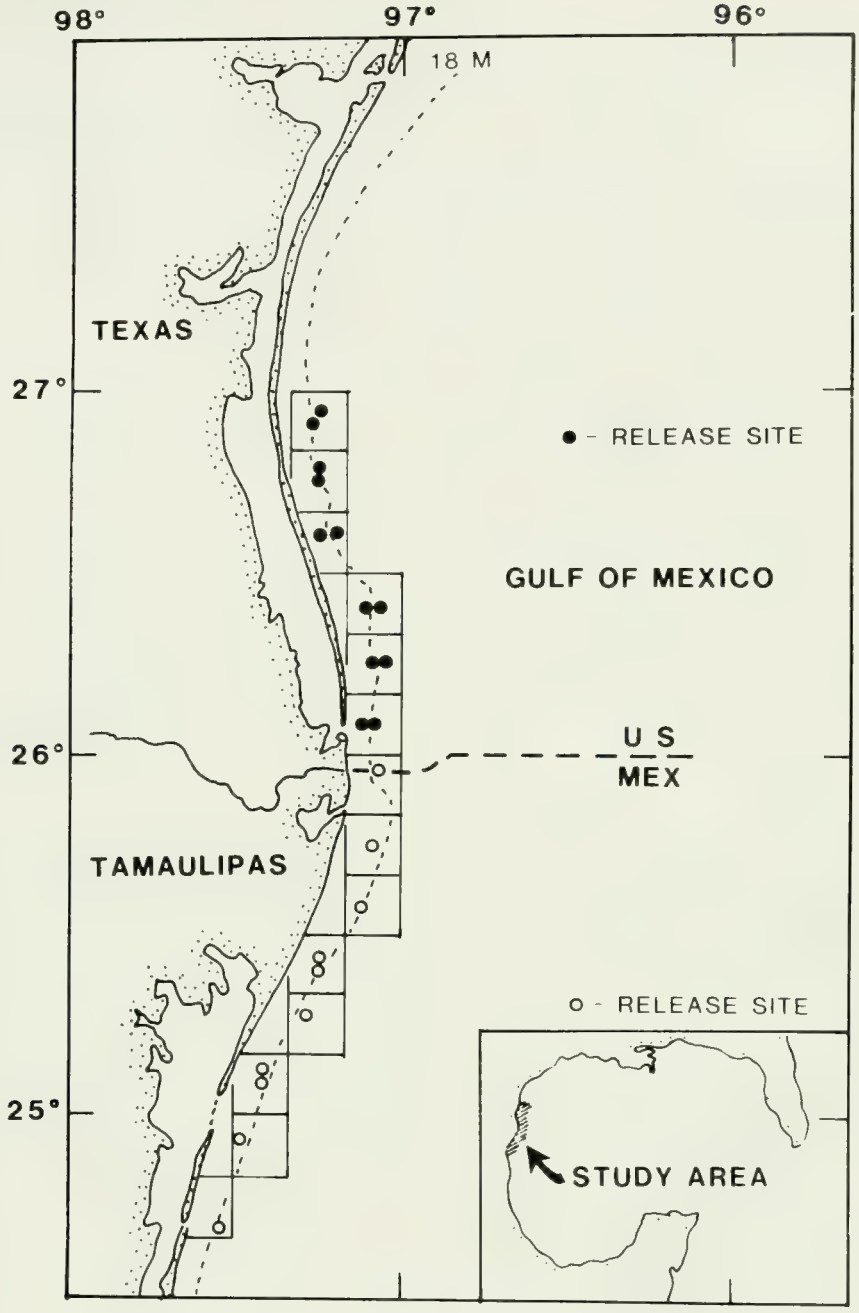

FIGURE 1.—Release sites for 1986 shrimp mark-recapture experiments.

TABLE 1.—Summary of 1986 mark-recapture experiments with brown shrimp and pink shrimp off Tamaulipas and Texas. Recaptures include all shrimp, regardless of the quality of return information, caught as of 5 December 1986, the date of last recapture.

State	Date	Release site	Number marked	Number released	Percent prerelease mortality	Number recaptured	Percent recaptured
Tamaulipas	5/30	25°36′N, 97°07′W	1,165	1,157	0.69	107	9.2
	5/31	25°17′N, 97°17′W	1,866	1,851	0.80	116	6.3
	6/1	25°24′N, 97°14′W	1,375	1,355	1.45	55	4.1
	6/2	25°57′N, 97°04′W	1,099	1,099	0.00	48	4.4
	6/3	24°41′N, 97°31′W	1,696	1,692	0.24	61	3.6
	6/4	24°56′N, 97°29′W	895	895	0.00	50	5.6
	6/5	25°06′N, 97°24′W	1,592	1,590	0.13	132	8.3
	6/6	25°08′N, 97°24′W	1,594	1,581	0.82	139	8.8
	6/7	25°26′N, 97°14′W	1,583	1,579	0.25	218	13.8
	6/8	25°45′N, 97°05′W	1,190	1,188	0.17	163	13.7
	5/30–6/8	— —	14,055	13,987	0.48	1,089	7.8
Texas	6/21	26°55′N, 97°17′W	2,305	1,931	16.26	163	8.4
	6/22	26°15′N, 97°03′W	1,995	1,898	4.36	434	22.9
	6/23	26°37′N, 97°11′W	3,188	3,024	5.14	583	19.3
	6/24	26°45′N, 97°15′W	991	939	5.25	140	14.9
	6/25	26°05′N, 97°07′W	3,288	3,157	3.98	873	27.7
	6/26	26°25′N, 97°07′W	3,690	3,661	0.79	327	8.9
	6/27	26°37′N, 97°11′W	1,784	1,729	3.08	307	17.8
	7/7	26°25′N, 97°06′W	2,009	1,993	0.80	242	12.1
	7/8	26°47′N, 97°15′W	2,063	2,056	0.34	276	13.4
	7/9	26°05′N, 97°05′W	3,617	3,600	0.47	458	12.7
	7/10	26°15′N, 97°04′W	2,447	2,399	1.96	444	18.5
	7/11	26°55′N, 97°17′W	1,864	1,849	0.80	303	16.4
	6/21–7/11	— —	29,241	28,236	3.44	4,550	16.1
Total			43,296	42,223	2.48	5,639	13.4

TABLE 2.—Comparison of shrimp species compositions for release, for all recaptures regardless of quality of return information, and for recaptures with complete and accurate return information. The latter group formed the data base for analyses of directional movement. N = number examined, * = significant difference (t-test, $\alpha = 0.05$) between proportions of brown shrimp released and recaptured (all recaptures excluding unknowns).

Release date	Release			All recaptures				Best recaptures		
	N	% brown	% pink	*N*	% brown	% pink	% unknown	*N*	% brown	% pink
5/30	297	30.6	69.4	107	15.9*	80.4	3.7	97	13.4	86.6
5/31	294	96.3	3.7	116	70.7*	24.1	5.2	102	74.5	25.5
6/1	289	92.1	7.9	55	92.7	5.5	1.8	49	93.9	6.1
6/2	299	87.0	13.0	48	85.4	10.4	4.2	21	95.2	4.8
6/3	297	37.0	63.0	61	70.5*	24.6	4.9	56	73.2	26.8
6/4	298	93.6	6.4	50	82.0	12.0	6.0	43	88.4	11.6
6/5	295	58.6	41.4	132	51.5	45.5	3.0	120	53.3	46.7
6/6	298	85.9	14.1	139	69.1*	23.0	7.9	106	75.5	24.5
6/7	296	31.1	68.9	218	29.4	62.4	8.3	119	35.3	64.7
6/8	299	59.2	40.8	163	6.1*	87.1	6.7	54	7.4	92.6
5/30–6/8	2,962	66.9	33.1	1,089	47.1*	47.1	5.8	767	55.3	44.7
6/21	279	21.1	78.9	163	6.7*	79.8	13.5	114	4.4	95.6
6/22	298	42.9	57.1	434	8.3*	72.6	19.1	288	9.4	90.6
6/23	298	8.4	91.6	583	2.6*	82.7	14.8	345	2.9	97.1
6/24	299	57.2	42.8	140	12.9*	77.9	9.3	81	19.8	80.2
6/25	292	22.9	77.1	873	9.5*	80.9	9.6	482	12.2	87.8
6/26	300	91.7	8.3	327	65.7	8.6	25.7	150	86.0	14.0
6/27	300	4.0	96.0	307	3.6	88.9	7.5	194	3.1	96.9
7/7	298	84.9	15.1	242	39.3	11.6	49.2	42	73.8	26.2
7/8	300	70.7	29.3	276	51.8*	38.0	10.1	43	58.1	41.9
7/9	299	85.6	14.4	458	57.9*	31.2	10.9	209	59.8	40.2
7/10	294	44.6	55.4	444	40.8	43.2	16.0	148	45.9	54.1
7/11	296	96.6	3.4	303	79.2	4.6	16.2	169	94.7	5.3
6/21–7/11	3,553	52.7	47.3	4,550	28.9*	55.5	15.6	2,265	29.2	70.8
Total	6,515	59.2	40.8	5,639	32.4*	53.9	13.7	3,032	35.8	64.2

tude, hereafter called "grids", along the Texas coast.

Port agents in Tamaulipas interviewed the captains of all vessels returning to the primary port of Tampico. Unknown, but assumed relatively small, amounts of catch and effort were potentially reported in more southerly ports. Interviewers collected catch and effort data by depth range and 10 minute lines of latitude between 22°N and 26°N. These data were then recordable either within 9 m depth zones or within grids as was done off Texas.

Interviews recorded effort by specific 9 m depth zones (Texas) or by actual depth ranges (Tamaulipas) per trip. Tamaulipas effort was assumed to fall equally into adjacent 9 m depth zones if more than one zone was covered by the stated depth range. The average fishing depth per trip was then calculated by weighting the hours expended in each 9 m depth zone by the middepth of that zone (e.g., the 10–18 m zone had a middepth of 14 m), summing over all depth zones, then dividing by the total effort expended on that trip. Average fishing depth for each fleet was then compared by a t-test corrected for unequal variances (Sokal and Rohlf 1969) using the average depth for each of 2,008 Texas trips and 505 Tamaulipas trips as observations.

Data Analysis

Three-factor, model I analysis of variance (ANOVA) with unequal cell sizes was employed to test hypotheses concerning the equivalence of treatment means for several types of observations on recaptured shrimp. The treatment factors were species (brown or pink), sex, and release state (Texas or Tamaulipas). State was chosen as a treatment because the level of fishing effort off Texas is much greater than that off Tamaulipas (approximately 200 vessels use the port of Tampico, whereas there are nearly 2,000 vessels registered in Texas alone). Four attributes of shrimp movement were examined by ANOVA: 1) distance travelled before recapture, assumed to be a straight line, 2) days at large, 3) apparent speed of movement, and 4) recapture depth. All four variables exhibited nonnormal (skewed) error distributions, as indicated by the Shapiro-Wilk test statistic (Shapiro and Wilk 1965), but the effects of nonnormality are thought to be minimal with large sample sizes (Underwood 1981). Variances of all variables were found to be heterogeneous (F-max test for unequal cell sizes; Sokal and Rohlf 1969). Data were $\log(x + 1)$-transformed prior to ANOVA (Underwood 1981), and F-max tests on transformed data indicated homogeneity of variances. Multiple comparison of treatment means of transformed data employed Fisher's LSD (least significant difference) because of unequal cell sizes (Milliken and Johnson 1984).

Circular scale data such as compass directions are a special type of interval scale data (Zar 1984) that cannot be examined by ANOVA because there is no physical reason for any zero point and high or low values are arbitrary (e.g., 45° is not a "larger" direction than 30°, and the mean of the 45° and 315° is not 180° but 0°). Examination of the raw data indicated that the assumption of unimodal distributions of recapture directions needed for hypothesis testing with the recommended parametric test (Watson-Williams statistic) would be violated. We conducted multisample testing of grouped directional data using contingency tables (Zar 1984). Before analysis, compass direction from release site to recapture site was adjusted downward by 20° off Texas and upward by 20° off Tamaulipas because northerly movement parallel to shore (hereafter termed "north") is 20° west of magnetic north (340°) off southern Texas and 20° east of magnetic north (020°) off northern Tamaulipas (Fig. 1). We grouped the adjusted directional data into eight arbitrary 45° divisions (0–44°, 45–89°, etc.) that fulfilled the requirement of having no expected cell frequency less than 4 (Zar 1984), with one exception. Only one brown shrimp and one pink shrimp released off Tamaulipas were recaptured between 270° and 359°; thus the contingency tables comparing these two data sets employed six 60° divisions (15–74°, 74–134°, etc.) to avoid low cell frequencies.

Differences in shrimp movement away from release sites were also tested by examining patterns in recaptures per unit fishing effort (R/f). R/f adjusts for temporal and spatial variations in fishing effort around each release site and integrates the effects of distance and direction travelled (Gitschlag 1986). For each release, recaptures per 10^4 hour of effort were calculated north, within, and south of the release grid from the release date through the end of the study period. "North" was defined as all grids lying between the northern latitude of the release grid and the northern latitude of the grid containing the northernmost recapture after each release. "South" was defined as all grids lying between the southern latitude of the release grid and the southern latitude of the grid containing the southernmost recapture after each release. "Within" was defined as the release grid and all grids directly east and west of it (recaptures in these grids did not show longshore movement). Two-factor, mixed model ANOVA with balanced cell sizes was

used to test the hypothesis that there were no detectable differences in shrimp recapture patterns for each species off each state as indicated by R/f values. This was a randomized complete blocks design for paired comparisons of R/f values as fixed treatments (north or south) and releases of tagged shrimp (10 off Tamaulipas, 12 off Texas) as randomly chosen blocks (Sokal and Rohlf 1969; Underwood 1981).

RESULTS

Releases and Recaptures

A total of 42,223 shrimp was marked and released between 30 May and 11 July 1986, with an overall recapture of 5,639 shrimp (13.4%) by 5 December 1986, the date of last recapture (Table 1). Over the entire recapture period, 50 brown shrimp and 62 pink shrimp marked off Tamaulipas were recaptured across the border in Texas waters, while 5 brown shrimp and 2 pink shrimp marked off Texas were recaptured off Tamaulipas. General mortality among tagged shrimp prior to daily releases totalled 2.48%. For no apparent reason, prerelease mortality was higher for the June releases off Texas (5.24%) than for those off Tamaulipas (0.48%) or off Texas in July (0.86%).

Brown shrimp represented 59.2% of the overall estimated species composition at release, while pink shrimp formed 40.8% (Table 2). There was considerable variation in species composition on a daily basis at any given site as well as among sites. The largest within-site differences were between 1 June and 7 June releases near 25°25′N off Tamaulipas (brown shrimp comprised 92% and 31%, respectively) and between 21 June and 11 July releases at 26°55′N off Texas (brown shrimp comprised 21% and 97%, respectively).

Species compositions at release and after recapture (excluding unknowns; Table 2) were significantly different for 12 of 22 release dates and over all releases in each state (*t*-test for equality of proportions, $\alpha = 0.05$; Sokal and Rohlf 1969). This is likely a reflection of differences in fishing effort: experimental shrimp were collected in 16–20 m waters while commercial shrimpers fished 5–90 m waters. Other factors could act and interact to cause these proportional changes in species composition including differential natural and tag-induced mortality, depth and substrate preferences, or catchability.

A total of 2,607 recaptures was excluded due to inconsistencies in recapture information cited previously. The remaining 3,032 "best" recaptures (Table 2) were used for all remaining analyses.

Components of Movement

Species, sex, and state had variable effects on the movements of recaptured shrimp, as indicated by distances travelled before recapture, days at large, speed, direction, and recapture depth. Distance travelled before recapture was significantly affected by both species and state (Table 3). The species × state interaction was also significant. Pink shrimp moved both the greatest and least mean distances of all eight groups, depending upon where they were released. Pink shrimp released off Tamaulipas moved an average of 29.5 km (males) or 29.0 km (females), distances that were significantly greater than those of pink shrimp released off Texas (males = 9.2 km, females = 9.8 km). Brown shrimp re-

TABLE 3.—Distances travelled by recaptured brown shrimp and pink shrimp. A. Three-factor, model I ANOVA using log (x + 1) - transformed data. B. Mean distances travelled. Underlined means are not significantly different (Fisher's LSD, $\alpha = 0.05$). B = brown shrimp, P = pink shrimp, F = female, M = male, Ta = Tamaulipas, Tx = Texas.

	df	SS	*F*	*P*
A. Source of variation				
Model	7	511.07	79.50	<0.001
Species	1	53.47	58.23	<0.001
Sex	1	0.13	0.14	0.705
State	1	441.94	481.24	<0.001
Species × sex	1	0.01	<0.01	0.948
Species × state	1	12.98	14.13	<0.001
Sex × state	1	0.15	0.16	0.686
Species × sex × state	1	2.40	2.61	0.106
Error	3024	2777.04		

B. Group:	PMTa	PFTa	BFTa	BMTa	BMTx	BFTx	PFTx	PMTx
Distance (km):	29.5	29.0	25.6	23.7	13.0	11.1	9.8	9.2

leased off Tamaulipas averaged significantly greater distances than brown shrimp released off Texas (23.7 and 25.6 km versus 11.1 and 13.0 km, respectively). The distributions of recaptures by distance travelled indicated that most Texas recaptures (70%) occurred within 20 km of release sites, while only 40% of the Tamaulipas recaptures were made at close range (Fig. 2). In all but one case, percentages of total Tamaulipas recaptures in any given distance category exceeded those of Texas recaptures.

Days at large were significantly affected only by the main effects of species, sex, and state (Table 4). Mean days at large were greater for shrimp released off Tamaulipas (16.4–20.2 days) than for shrimp released off Texas (11.8–14.4 days), and within each state brown shrimp tended to be at large longer than pink shrimp. Within each species-state group, female shrimp remained at large longer than male shrimp. The distributions of recaptures by days at large indicated that 65–85% of all Texas recaptures were made 1–19 days after release, whereas only 45–50% of Tamaulipas recaptures occurred during this time period (Fig. 3). Proportions of brown shrimp recaptures in the 40–79 days at large categories were also greater than those of pink shrimp.

Movement speeds of recaptured shrimp were affected by the interaction of species and state (Table 5). This was reflected both in the significant main effect of state (shrimp released off Tamaulipas moved faster than those released off Texas, 1.67–2.34 km/d versus 1.04–1.25 km/d) and in the species × state interaction (pink shrimp released off Tamaulipas had significantly greater speeds than pink shrimp released off Texas, and the same trend was found for brown shrimp). The majority of all shrimp recaptured exhibited speeds of less than 1 km/d (Fig. 4). However, recaptures of shrimp released off Tamaulipas usually had proportionally more shrimp with speeds exceeding 4 km/d.

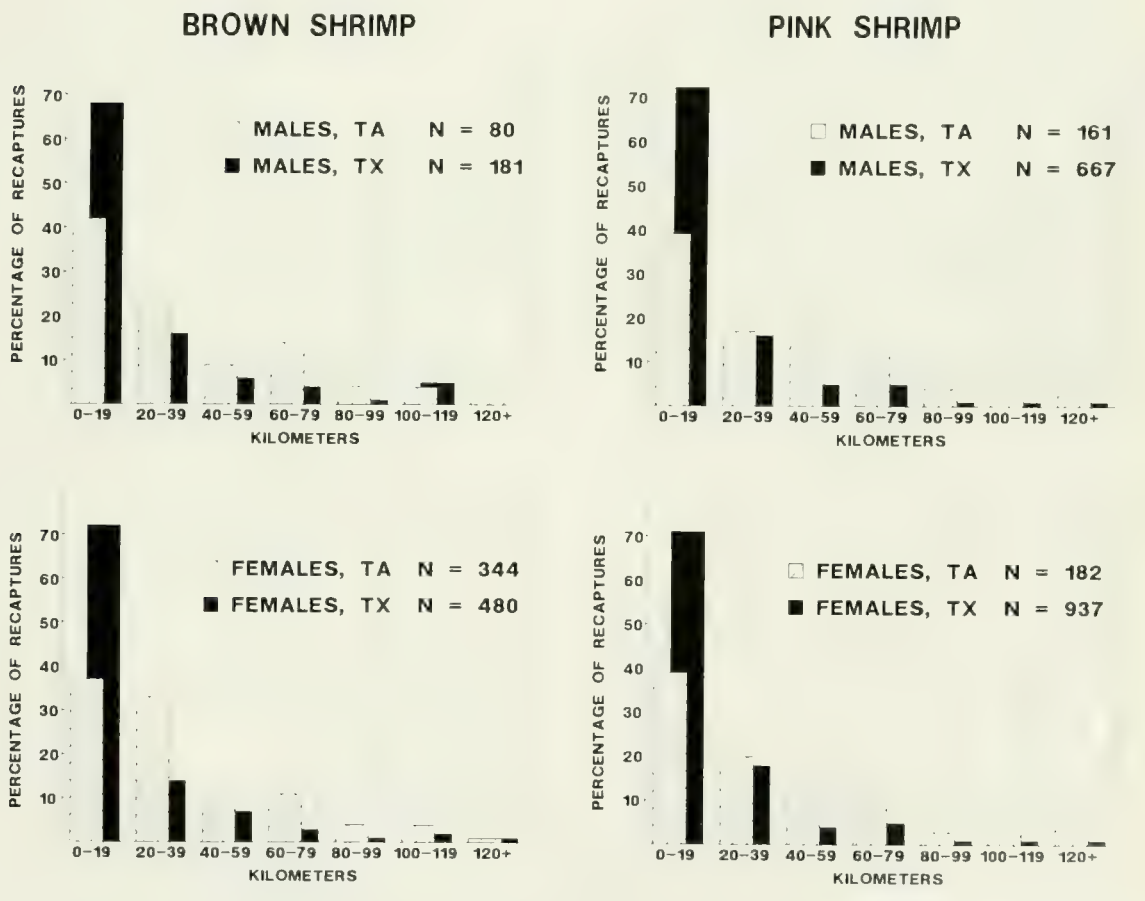

FIGURE 2.—Comparison of distances travelled by recaptured shrimp after release off Tamaulipas (TA) or Texas (TX).

TABLE 4.—Days at large for recaptured brown shrimp and pink shrimp. A. Three-factor, model I ANOVA using log (x + 1) - transformed data. B. Mean days at large. Underlined means are not significantly different (Fisher's LSD, α = 0.05). B = brown shrimp, P = pink shrimp, F = female, M = male, Ta = Tamaulipas, Tx = Texas.

	df	SS	*F*	*P*
A. Source of variation				
Model	7	84.86	27.18	<0.001
Species	1	31.81	71.33	<0.001
Sex	1	2.02	4.53	0.033
State	1	50.55	113.35	<0.001
Species × sex	1	0.18	0.41	0.520
Species × state	1	0.16	0.36	0.550
Sex × state	1	0.13	0.29	0.592
Species × sex × state	1	<0.01	<0.01	0.999
Error	3024	1348.66		

B. Group:	BFTa	BMTa	PFTa	PMTa	BFTx	BMTx	PFTx	PMTx
Days at large:	20.2	19.7	16.9	16.4	14.4	13.6	12.6	11.8

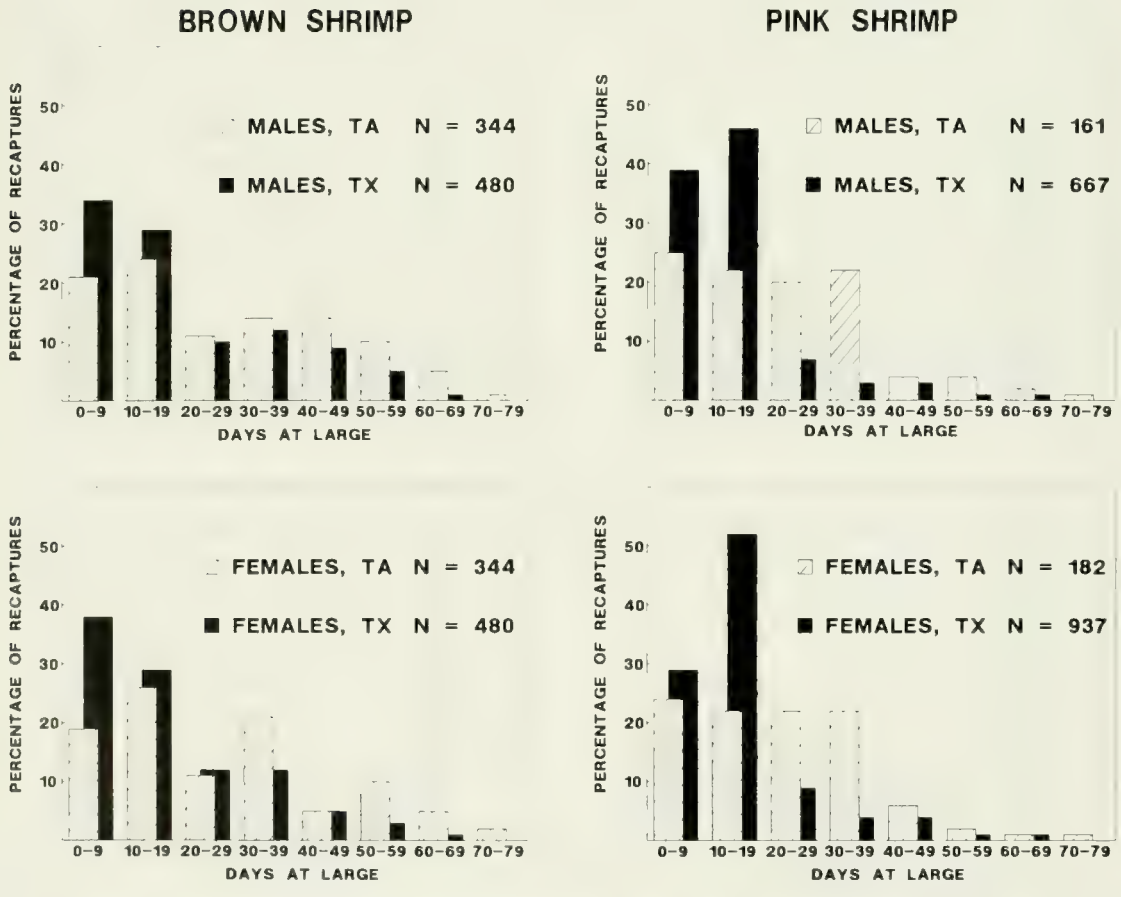

FIGURE 3.—Comparison of days at large for recaptured shrimp after release off Tamaulipas (TA) or Texas (TX).

TABLE 5.—Apparent movement speeds of recaptured brown shrimp and pink shrimp. A. Three-factor, model I ANOVA using log (x + 1) - transformed data. B. Mean speeds. Underlined means are not significantly different (Fisher's LSD, α = 0.05). B = brown shrimp, P = pink shrimp, F = female, M = male, Ta = Tamaulipas, Tx = Texas.

	df	SS	F	P
A. Source of variation				
Model	7	81.53	28.19	<0.001
Species	1	1.54	3.73	0.054
Sex	1	0.41	1.00	0.317
State	1	71.75	173.68	<0.001
Species × sex	1	0.04	0.10	0.749
Species × state	1	7.55	18.28	<0.001
Sex × state	1	<0.01	0.01	0.931
Species × sex × state	1	0.23	0.55	0.459
Error	3024	1249.30		

B. Group:	PMTa	PFTa	BMTa	BFTa	BMTx	BFTx	PFTx	PMTx
Speed (km/d):	2.34	2.24	1.73	1.67	1.25	1.07	1.04	1.04

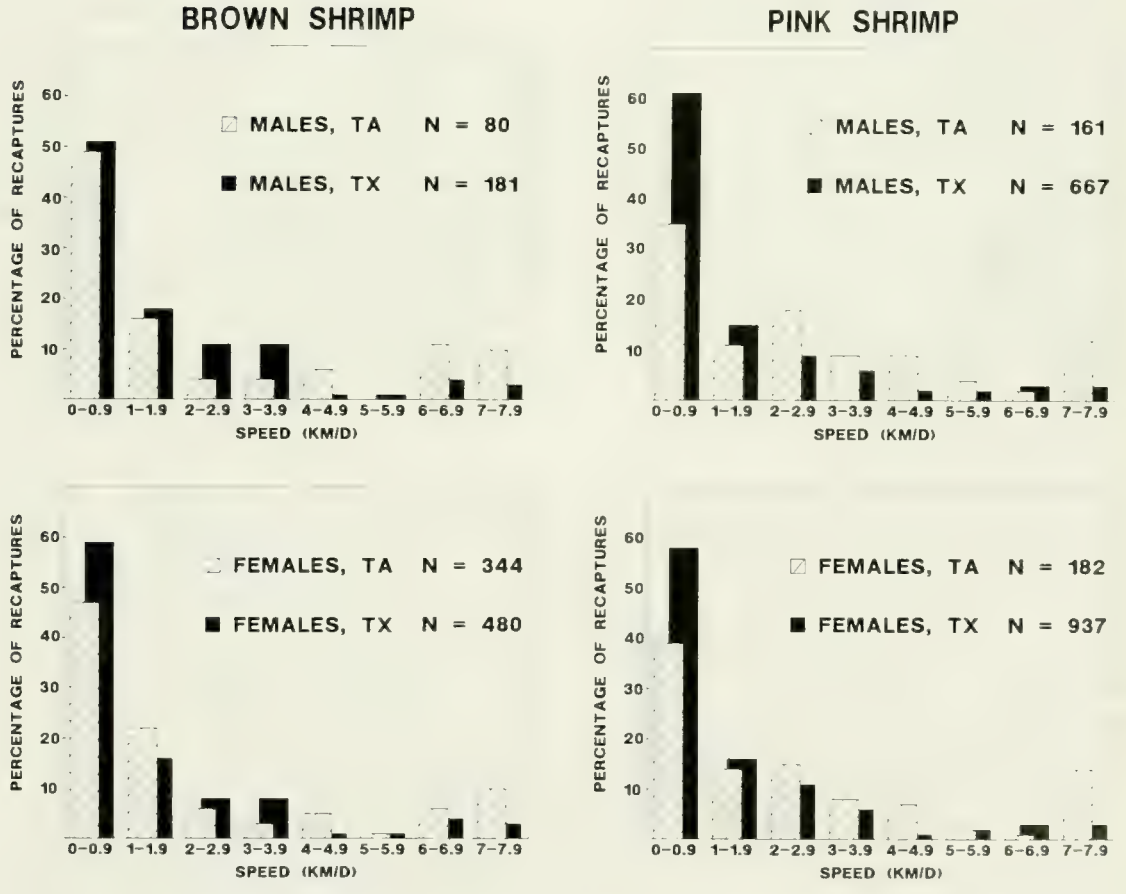

FIGURE 4.—Comparison of movement speeds of recaptured shrimp after release off Tamaulipas (TA) or Texas (TX).

Directional movement patterns of brown shrimp and pink shrimp were influenced by species and state (Table 6). The full three-factor model indicated significant differences ($P < 0.001$) in the frequency distributions of recaptures. Analysis of single factors indicated that recapture patterns based on sex alone were not significantly different. The significant species × state interaction could not be resolved further, since partitioning this interaction to within-state or within-species components still yielded significant differences in the distributions of recapture frequencies (Table 6). Graphical presentation of these analyses (Fig. 5) illustrated several points: 1) pink shrimp tended to orient alongshore (north and south) while brown shrimp had a strong offshore component (NE-SE); 2) male shrimp and

TABLE 6.—Analysis of adjusted directional movement of recaptured brown shrimp and pink shrimp using contingency tables. Directions were grouped into 45° divisions of the compass (0–44°, 45–89°, etc.) except where noted by an asterisk(*) when 60° sectors were formed (15–74°, 75–134°, etc.).

Factors	df	χ^2	P
Species × sex × state	49	1,593.63	<0.001
Species × state	21	1,569.89	<0.001
Species × Texas	7	109.15	<0.001
Species × Tamaulipas	5*	41.61	<0.001
Brown × state	7	465.39	<0.001
Pink × state	7	933.68	<0.001
Species	7	186.91	<0.001
Sex	7	5.71	0.573
State	7	1,400.36	<0.001

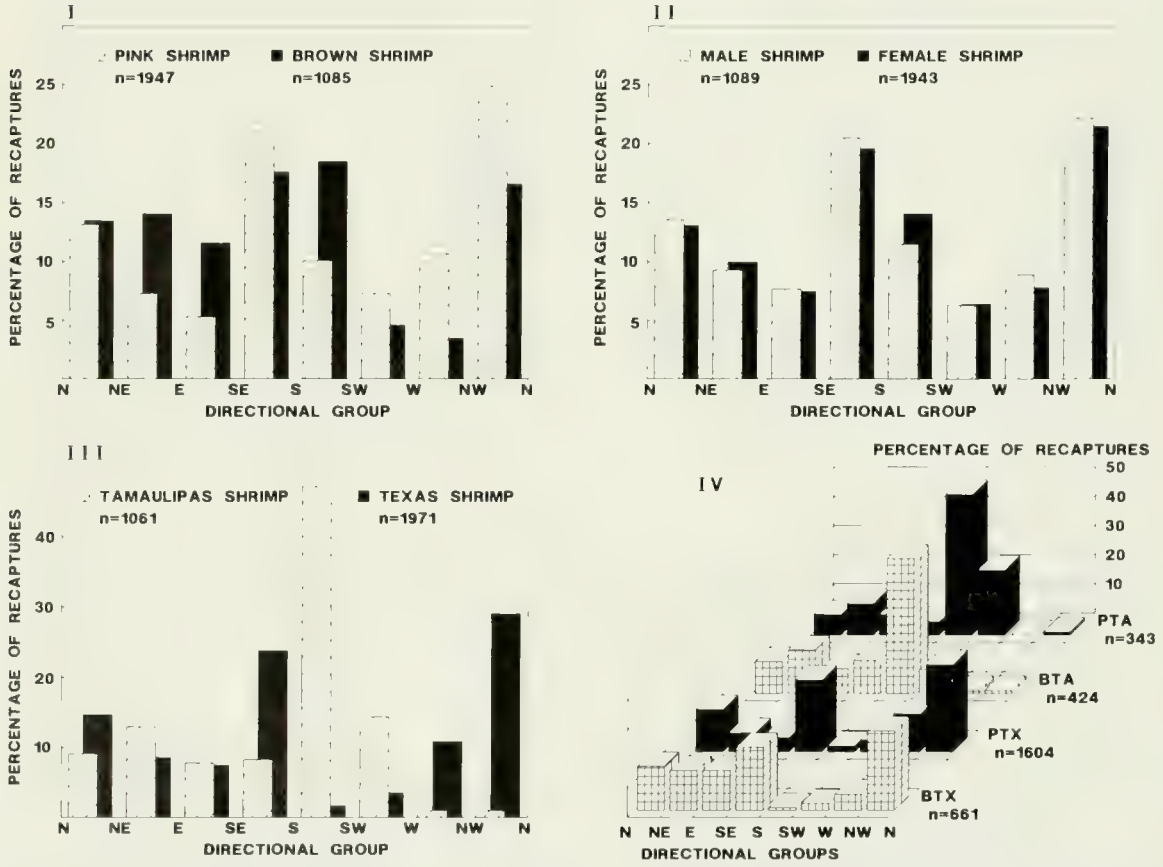

FIGURE 5.—Comparison of adjusted compass headings of recaptured brown shrimp (B) and pink shrimp (P) released off Tamaulipas (TA) and Texas (TX), where directional groups fall between compass points. n = number of recaptures. I. Frequencies by species. II. Frequencies by sex. III. Frequencies by state. IV. Frequencies by species × state interaction.

female shrimp exhibited similar recapture patterns; and 3) recaptures after Tamaulipas releases exhibited strong southward directionality and weak westerly to northerly movement compared with recaptures after Texas releases.

Recapture depth was significantly influenced by the main effects of species and state, but no interaction terms were significant (Table 7). Although all shrimp were released at 18 m depths, mean recapture depths of brown shrimp were greater than those for pink shrimp (21.5–24.0 m versus 19.6–21.5 m, respectively). Within each species, shrimp released off Tamaulipas moved to deeper waters than did shrimp released off Texas, and within each state brown shrimp moved to significantly deeper waters than pink shrimp. Most recaptures were made within 16–20 m depths, a trend that was stronger for pink shrimp than for brown shrimp (Fig. 6). Brown shrimp were more frequently recaptured in 21–25 m and 26–30 m waters than were pink shrimp.

Commercial Fishing Patterns

A total of 57,511 hours of fishing effort was recorded through interviews of fishermen landing at Tampico during the survey period, with resultant landings of 459.4 t of exportable shrimp tails. An additional 262.7 t (36% of total catch) of "pacotilla" or undersized, non-exportable shrimp tails were also landed (Castro[4]). Primary fishing areas were lat. 22°–23°N and 24°–25°N where Tamaulipas effort was concentrated off river mouths or lagoon passes (Fig. 7).

Interviews of seafood processors and of vessels landing in U.S. ports after fishing off Texas during 1 June–31 August 1986 indicated a total fishing effort of 432,175 hours with landings of 6,479 t of shrimp tails (NMFS, unpubl. data). Actual interviews of fishermen comprised 239,006 hours and 3,614 t of those totals. Logbooks kept by 47 Texas shrimp vessels (a subset of interviews) recorded 13,501 hours and 190 t; thus the detailed logbook data represented 3.1% of the total effort and 2.9% of the total landings from Texas waters. Logbook data were used to apportion total fishing effort off Texas into grids. Texas effort was more diffuse and was not clustered around river mouths or estuary passes as it was off Tamaulipas (Fig. 8).

Both fisheries operated in 1–82 m waters, of which Texas has approximately 2.3 times the continental shelf area as does Tamaulipas (U.S. Department of Commerce, NOS Chart 411). Comparison of the depth distributions of fishing effort between American and Mexican fleets (illustrated in Figure 9) indicated that American fishermen expended significantly more effort in shallower waters than did Mexican fishermen (mean fishing depths were 33.8 m and 35.1 m, respectively; t-test, $P = 0.009$). Overall catch rates were higher in Texas waters (6,479 t/432,175 h = 15.0 kg/h) than in Tamaulipas waters (722 t/57,511 h = 12.6 kg/h). Data collected concerning fishing gear indicated that vessels in both fleets generally employed four 12 m nets (mesh size data were unavailable).

[4]Castro M., R. G. Informe de actividades del programa MEX-US Golfo, grupo camaron Mexico. Programa MEX-US Golfo 1986. Unpubl. manuscr., 18 p. Instituto Nacional de la Pesca, Centro Regional de Investigaciones Pesqueras, Tampico, Tamaulipas, Mexico.

TABLE 7.—Recapture depth for brown shrimp and pink shrimp released in 18 m waters. A. Three-factor, model I ANOVA using log (x + 1) - transformed data. B. Mean recapture depths. Underlined means are not significantly different (Fisher's LSD, $\alpha = 0.05$). B = brown shrimp, P = pink shrimp, F = female, M = male, Ta = Tamaulipas, Tx = Texas.

	df	SS	F	P
A. Source of variation				
Model	7	13.18	35.12	<0.001
Species	1	8.84	164.94	<0.001
Sex	1	<0.01	0.13	0.722
State	1	4.15	77.36	<0.001
Species × sex	1	<0.01	0.17	0.682
Species × state	1	0.11	2.01	0.157
Sex × state	1	0.02	0.43	0.510
Species × sex × state	1	0.04	0.83	0.361
Error	3024	162.13		

B. Group:	BFTa	BMTa	BMTx	BFTx	PMTa	PFTa	PFTx	PMTx
Depth (m):	24.0	23.8	21.6	21.5	21.5	21.0	19.7	19.6

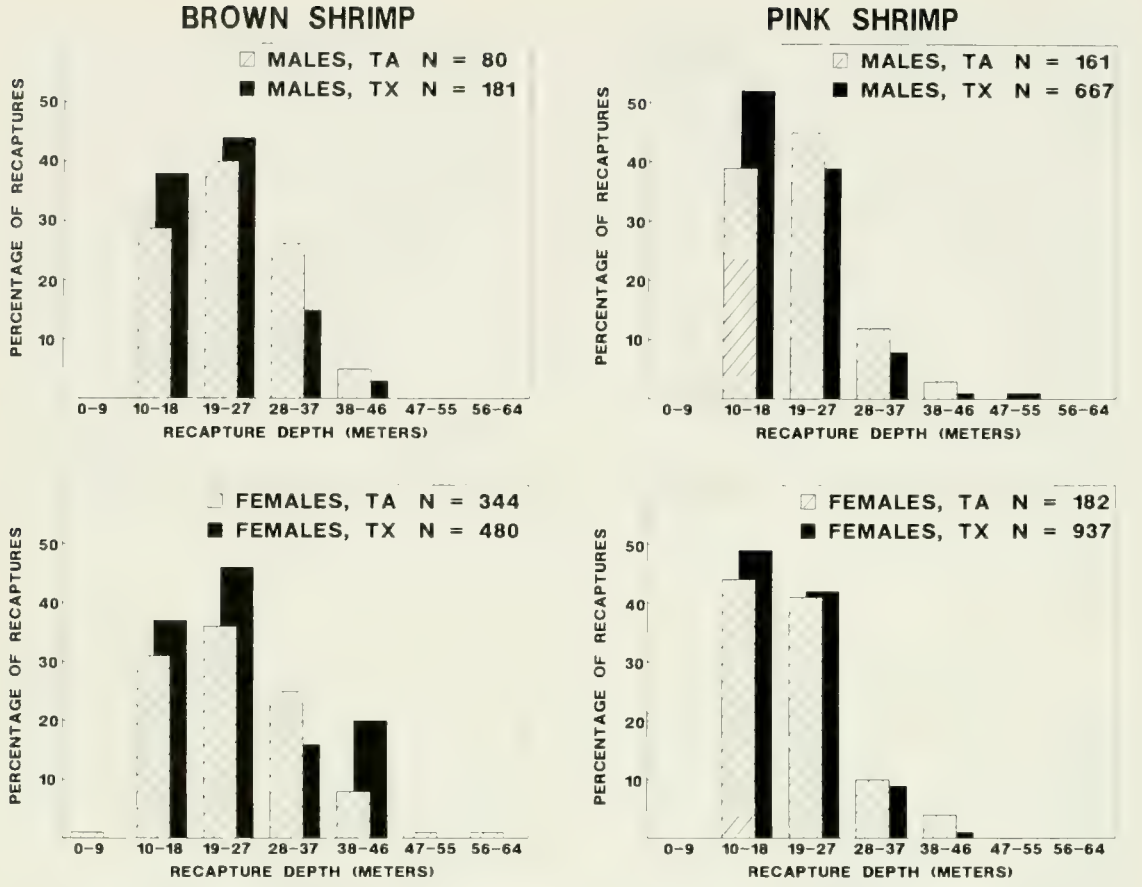

FIGURE 6.—Comparison of recapture depths of marked shrimp after release off Tamaulipas (TA) or Texas (TX).

R/f Analysis

Previous analyses indicated that sex had little to do with components of shrimp movement (except in some three-way interaction terms), so sexes were pooled for R/f analysis. North versus south comparisons of cumulative R/f values after each brown shrimp release (Table 8) indicated greater movement toward the border after 5 of 10 Tamaulipas releases and after 9 of 12 Texas releases. However, there were no significant differences in north versus south R/f values for brown shrimp in either state (Table 9). Comparisons of R/f values after pink shrimp releases indicated greater movement toward the border after 8 of 10 Tamaulipas releases and after 6 of 12 Texas releases (Table 8). Only pink shrimp released off Tamaulipas exhibited significant northward movement (Table 9).

Replicate releases on different dates were made at two sites off Tamaulipas and at all six sites off Texas (Table 8). The recapture patterns indicated that shrimp collected near, and released on, a given site did not always disperse in the same directions. Only in 6 of 8 brown shrimp releases and 4 of 8 pink shrimp releases were the paired R/f values higher in the same directions.

DISCUSSION

Variation in components of movement was linked to both species and release state. However, R/f values indicated that during the study period recaptured brown shrimp exhibited no preferred movement north or south off either Texas or Tamaulipas while recaptured pink shrimp only showed significant movement northward after Tamaulipas releases. Thus, the 1986 Texas fishery did not lose fishable biomass across the border as a result of the Texas Closure and, in fact, may have gained biomass due to the northward movement of pink shrimp off

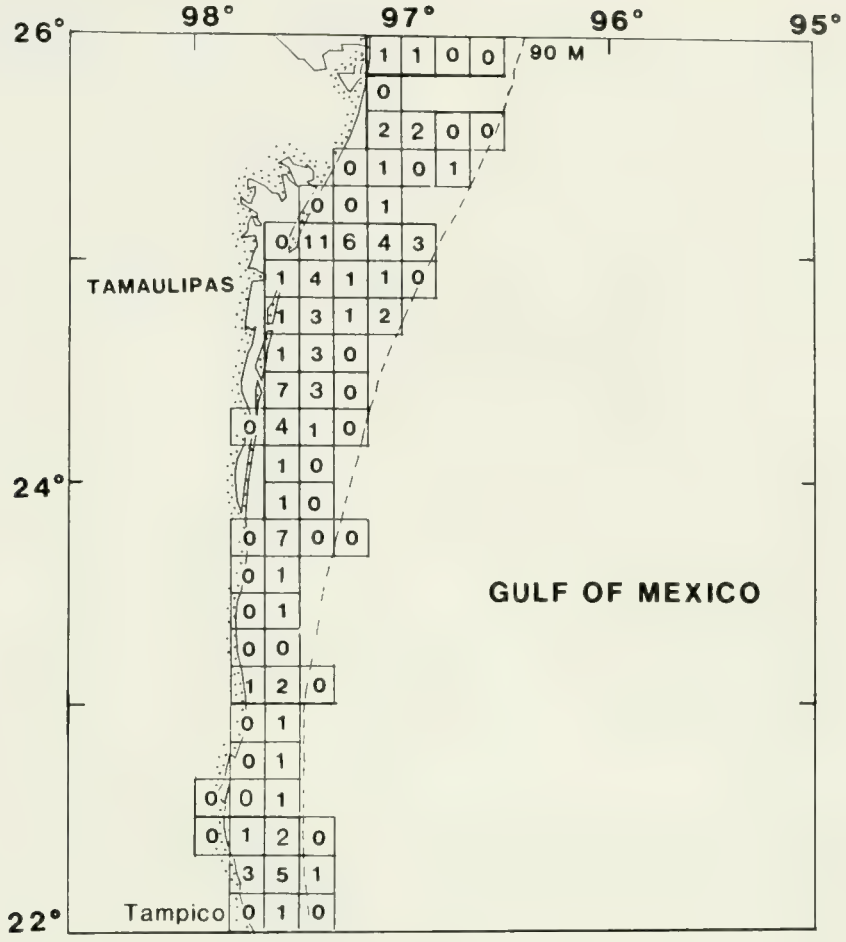

FIGURE 7.—Distribution of fishing effort by 10-minute grids of latitude and longitude for vessels fishing off Tamaulipas and landing in Tampico during 1 June–31 August 1986. Numbers in each grid are percentages of the total effort recorded by port agent interviews, where 0 = <1% of the total effort and a blank = no effort.

TABLE 8.—Directional movement of brown shrimp and pink shrimp away from Tamaulipas (TA) and Texas (TX) release sites as indicated by recaptures per 10^4 hour fished (R/f) north and south of the release sites. Sites are arranged from south to north, and an asterisk (*) indicates a replicate release.

Release		Brown shrimp R/f		Pink shrimp R/f		Release		Brown shrimp R/f		Pink shrimp R/f	
State	Site	North	South	North	South	State	Site	North	South	North	South
TA	1	2.7	23.1	1.7	7.2	TX	1	2.0	6.4	20.8	515.5
	2	5.9	7.2	2.2	0.5		1*	9.4	16.7	64.3	0.0
	3	3.2	15.1	11.7	13.8		2	1.9	6.2	10.8	83.3
	3*	13.7	13.9	7.8	4.9		2*	1.8	48.0	3.5	6.0
	4	63.2	11.3	24.8	2.0		3	2.9	13.7	2.3	0.0
	5	46.0	11.4	5.4	0.7		3*	0.9	2.0	0.0	1.4
	5*	38.0	9.3	48.9	16.0		4	0.7	1.4	13.4	17.0
	6	0.0	3.4	23.3	11.0		4*	1.1	0.6	18.7	10.2
	7	8.1	1.8	48.4	11.2		5	0.8	0.0	1.9	0.5
	8	3.7	0.0	0.1	0.0		5*	10.6	0.6	3.7	0.0
							6	0.0	1.2	1.0	6.9
							6*	3.3	15.4	0.8	0.7

TABLE 9.—ANOVA results comparing paired north versus south R/f values for brown shrimp and pink shrimp by release state (TA = Tamaulipas, TX = Texas).

Species	State	Source of error	df	SS	F	P
Brown	TA	R/f	1	389.84	1.53	0.247
		Release	9	2,612.93	1.14	0.424
		Error	9	2,290.03		
	TX	R/f	1	245.76	2.57	0.137
		Release	11	1,125.21	1.07	0.456
		Error	11	1,050.57		
Pink	TA	R/f	1	572.45	5.00	0.048
		Release	9	2,378.55	2.31	0.114
		Error	9	1,030.27		
	TX	R/f	1	10,429.20	0.98	0.343
		Release	11	125,748.12	1.08	0.452
		Error	11	116,704.83		

Tamaulipas. Previous mark-recapture studies in Texas and Tamaulipas waters indicated southward movement of brown shrimp and pink shrimp after May–June 1979 and 1980 releases in areas adjoining the border (Sheridan et al. 1987). Analysis of recaptures from those early experiments employed different methods from that used in this paper. First, recaptures "north", "within", and "south" of the release sites were located in relatively large areas delimited by one degree of latitude or longitude and by 0–90 m depths, not 10 minute grids of latitude and longitude; thus short-distance movement was not included in the analyses. Second, recaptures were standardized by landings within these large areas, not by effort. Third, recaptures and landings were accepted from the month of release through the month of last recapture, not during a restricted time period, which tended to reduce recaptures per unit landings values since ≥50% of

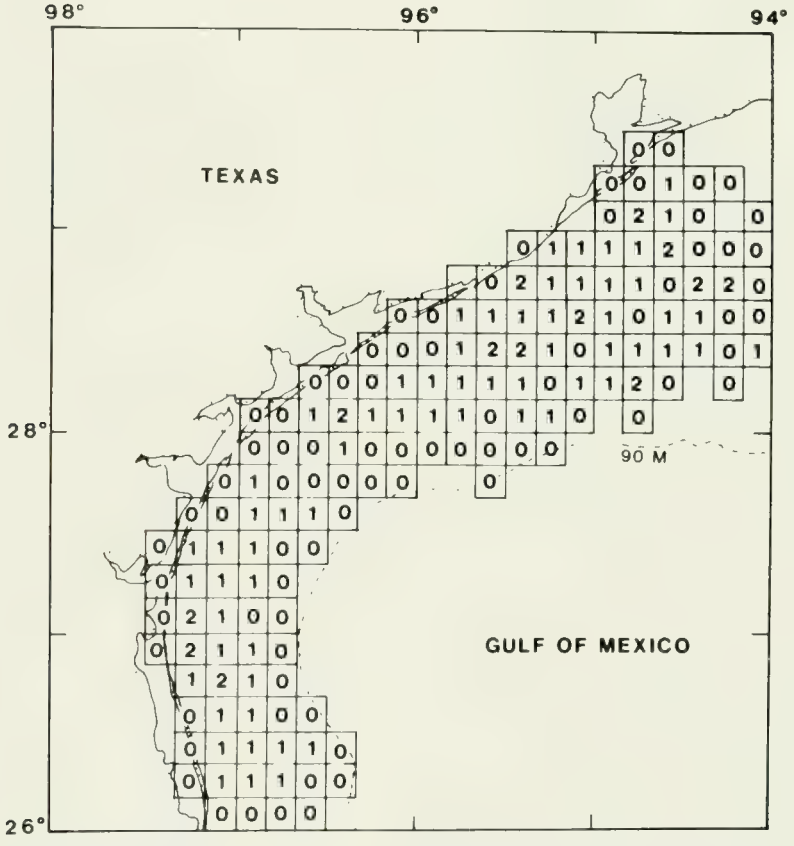

FIGURE 8.—Distribution of fishing effort by 10-minute grids of latitude and longitude for 47 vessels fishing off Texas during 1 June–31 August 1986. Numbers in each grid are percentages of total log book effort, where 0 = <1% and a blank = no effort.

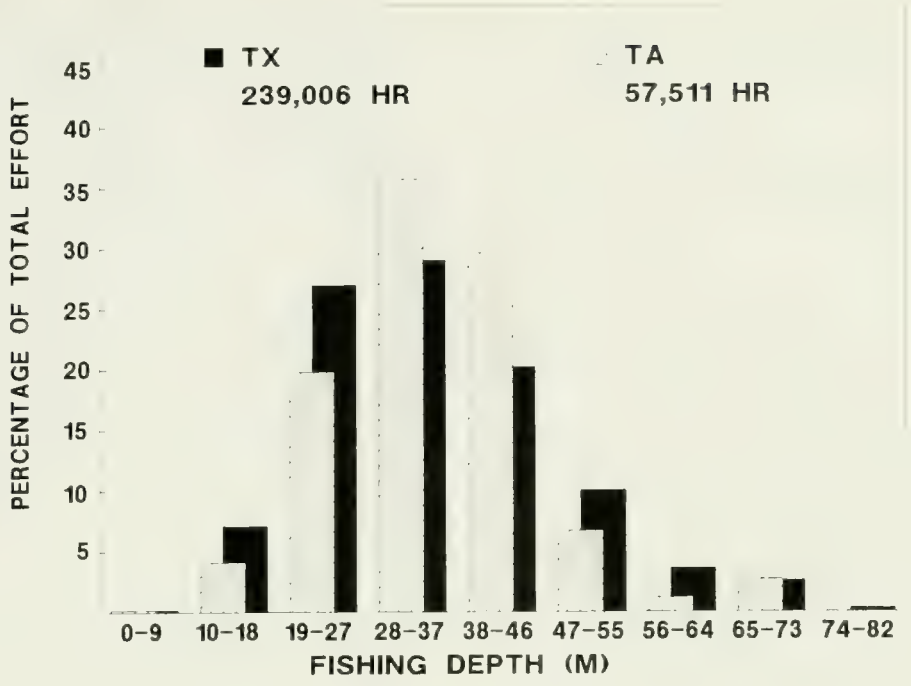

FIGURE 9.—Comparison of fishing effort (h) by depth strata between Texas (TX) and Tamaulipas (TA) interviews.

all recaptures were made within 40 days after release. Thus, in contrast to the present study, the mark-recapture analyses reported by Sheridan et al. (1987) were of limited use since they described primarily a small number of long-distance, long-duration recaptures. The difference in results is most likely due to the higher quality, finer scale data collected during the present experiments and to the use of all recaptures, not just those for shrimp moving long distances.

The factors "species" and "state" may actually describe different habitat requirements and different levels of fishing effort in the western Gulf of Mexico. Trawl catches indicate brown shrimp utilize a greater depth range (0–160 m) and are found over a wider variety of substrates (sand, silt, clay) than pink shrimp (0–65 m depth; coarse sand and shell) (Hildebrand 1954, 1955; Williams 1958; Cook and Lindner 1970; Costello and Allen 1970; Grady 1971; Renfro and Brusher 1982). Offshore substrate preferences of brown shrimp and pink shrimp have not been directly tested, however. Coarse substrates tend to lie in pockets or bands paralleling the Texas coast (McGowen and Morton 1979); thus pink shrimp recaptures could reflect longshore movement seeking these substrates. The major influence on recapture patterns was the difference in fishing activity between the two states: fishing effort off Tamaulipas was only 13% of the effort expended off Texas and occurred in deeper waters. Consequently, fishing mortality off Tamaulipas was lower and tagged shrimp generally exhibited a lesser recapture rate, greater times at large, greater distances travelled, and greater depths at recapture. Collection and utilization of fishing effort data thus seems imperative for interpretation of tag recapture patterns.

A potential source of error common to all mark-recapture experiments involves the precision of reported recapture locations. Trawl tows are of variable durations and distances, and there is no way of knowing at what point along a towing track that a marked shrimp is captured. In addition, the exact locating of recoveries depends on the precision of navigational equipment, which is usually not recorded and which could vary from dead reckoning to satellite navigation. These factors would affect estimates of distance travelled, speed, and direction but not recapture depth (shrimpers tow along, rather than across, depth contours to avoid gear adjustments) or days at large. Effects on R/f values

would also be minimal since R/f does not depend on exact distances. There was no way to control for these potential difficulties other than discarding all short-distance returns, and that would have resulted in a loss of 1,173 of the 3,032 most accurate recaptures. It was believed that the initial screening of recaptures, which eliminated 2,607 of 5,639 recaptures, removed most of the inaccurate return data.

Another source of error relates to the estimated distribution of fishing effort into the grid system off Mexico. Interview coverage was 100% of all vessels coming into the port of Tampico, Tamaulipas, and likely reached a majority of Mexican vessels fishing off Tamaulipas. Captains were asked to specify fishing areas and effort but not how much time was spent in each grid. If more than one grid was fished on a trip, it was assumed that effort was divided equally among all grids fished. This would tend to reduce the estimated effort over more favored fishing grounds and increase it elsewhere, inflating R/f values over favored grounds and decreasing R/f values elsewhere. In Tamaulipas waters, effort appeared to be most concentrated between 24°20′N and 25°09′N off the Laguna Madre de Tamaulipas. Six of 10 releases were made to the north (25°10′N–25°59′N) and R/f values north of these 6 release sites could have been artificially low. This would not affect the already significant northward trend in pink shrimp movement, but would increase the nonsignificant trend in northward brown shrimp movement toward significance.

A different problem exists with the estimated distribution of fishing effort off Texas. Whereas the captains of nearly 100% of the Tamaulipas fleet were interviewed, only 3.1% of those of the Texas fleet were interviewed (via logbooks) in enough detail to estimate effort in grids. Regular port agent interviews recorded 55% of total Texas effort. Comparison of the depth distributions of effort between Texas interviews and Texas logbooks indicated no significant differences. However, comparison of the effort expended within one-degree quadrangles of latitude and longitude determined by each method indicated similar estimations of effort from 26°00′N to 26°59′N (32% of total effort by logbook, 33% by interview) but overestimation of effort from 27°00′N to 27°59′N by logbooks (38% vs. 25%). For Texas releases with recaptures north of 26°59′N (9 of 12 releases), R/f values north of release sites were probably underestimated. Since neither brown shrimp nor pink shrimp R/f values indicated significant directional movement off Texas, it is unlikely that the underestimation of northward R/f values would affect the comparisons.

Recaptures standardized by fishing effort are rarely used to analyze movement patterns of aquatic organisms. Bayliff and Rothschild (1974) and Bayliff (1979) reported movements of yellowfin tuna, *Thunnus albacares*, in terms of recaptures weighted by fishing effort in the eastern Pacific Ocean (Mexico to Ecuador). Their recapture patterns were not tested for directional movement after individual releases, and interpretation of their results could be confounded by long recapture periods (up to one year) and the large ocean surface areas addressed (0°–25°N, 80°–150°W). Gitschlag (1986) employed the R/f index as a means of reducing bias associated with nonuniform fishing effort upon apparent movement patterns of pink shrimp in an area approximating a quadrangle of one degree latitude and longitude off Florida. The only other study reporting both recaptures and effort for marked shrimp was conducted by Somers and Kirkwood (1984) on tiger prawn (*Penaeus esculentus* and *P. semisulcatus*) movements in Australia, but recaptures per unit effort were not analyzed. In reality, most mark-recapture experiments on penaeid shrimp and other organisms have been more concerned with obtaining estimates of fishing and natural mortality rates, growth rates, or stock ranges rather than assessing movements per se. We believe that employing R/f values yields more accurate information on shrimp movements than recaptures alone.

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POPULATION BIOLOGY OF RED ABALONES, *HALIOTIS RUFESCENS*, IN SOUTHERN CALIFORNIA AND MANAGEMENT OF THE RED AND PINK, *H. CORRUGATA*, ABALONE FISHERIES

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ABSTRACT

Population dynamics of red abalones, *Haliotis rufescens* Swainson, were studied at Johnsons Lee, Santa Rosa Island, California from 1978 through 1982 and in 1984. Tagging studies were used to calculate the von Bertalanffy growth parameters. Size-frequency distributions were used to assess settlement rate and fishable stock, and to estimate the natural mortality rate. These results were employed in yield-per-recruit and egg-per-recruit analyses; similar calculations were made for pink abalones, *H. corrugata* Gray, using values from the literature. Our analyses suggest that present sport and commercial minimum legal sizes allow for adequate egg production to maintain stock sizes; simple recruitment overfishing is not a satisfactory explanation for the sharp and continuing decline in landings of both species. We consider other factors which may be responsible and argue that prudent abalone management should maintain egg-per-recruit at the cost of some potential yield.

The red abalone, *Haliotis rufescens* Swainson, is the largest member of its genus and historically the most important species in the California abalone fishery. Ranging from Coos Bay, OR to Bahia Tortugas, Baja California (Cox 1962), red abalones are found along the entire coast of California but almost all of the commercial harvest comes from Point Conception south (Fig. 1). The recovery of the sea otter, *Enhydra lutris*, population has precluded the commercial fishery within its central California range (Miller and Geibel 1973; Hardy et al. 1982; Estes and Van Blaricom 1985) and the north coast has been reserved for the recreational fishery since 1945 (Cicin-Sain et al. 1977). Today the major commercial red abalone fishing grounds are in southern California—the northern Channel Islands, Santa Cruz, San Miguel, San Nicolas, and Santa Rosa Islands—and mainland sites where upwelling produces cooler temperatures which are north and west of Santa Barbara and near San Diego. Red abalones are also found on the Palos Verdes Peninsula within the coastal area closed to all abalone fishing. The present size limits are 178 mm for the recreational fishery and 197 mm for commercial harvest.

The pink abalone, *H. corrugata* Gray, is found from Point Conception, CA (Cox 1962) to Punta Abreojos, Baja California (Doi et al. 1977). From 1949 to 1970, pink abalones supported a fishery equal in importance to the red abalone fishery. In 1970, an increase in the minimum legal commercial size from 152 to 159 mm caused a sharp decrease in landings (Tegner 1989). The present size limits are 152 mm for sport and 159 mm for commercial harvesters.

Despite the high landed value and the recreational importance of the abalone fishery in California, no stock assessments are available. Management has been based on the assumption that an appropriate size limit will protect the stocks. An appropriate size limit is considered to be one large enough to allow sublegal abalones to spawn several times before being recruited to the fishery, yet small enough that the size is attained within a reasonable number of years after settlement (Burge et al. 1975). A strong dependence on a minimum size limit is consistent with abalone fishery management elsewhere. In his review of world abalone fisheries, Harrison (1986, p. 21) suggested that "an appropriate set of effectively policed minimum size regulations is the cornerstone of managing these fisheries." Despite the importance of the size limit in managing California abalone fisheries, no analysis of its effect on population dynamics or fisheries yield has been published.

After many years of relative stability, the red and pink abalone harvests began a marked decline in the late 1960s (Burge et al. 1975; Cicin-Sain et al. 1977). Despite limitation of entry to the commercial fishery and tighter restrictions on the recreational fishery in the mid-1970s, the decline in landings has con-

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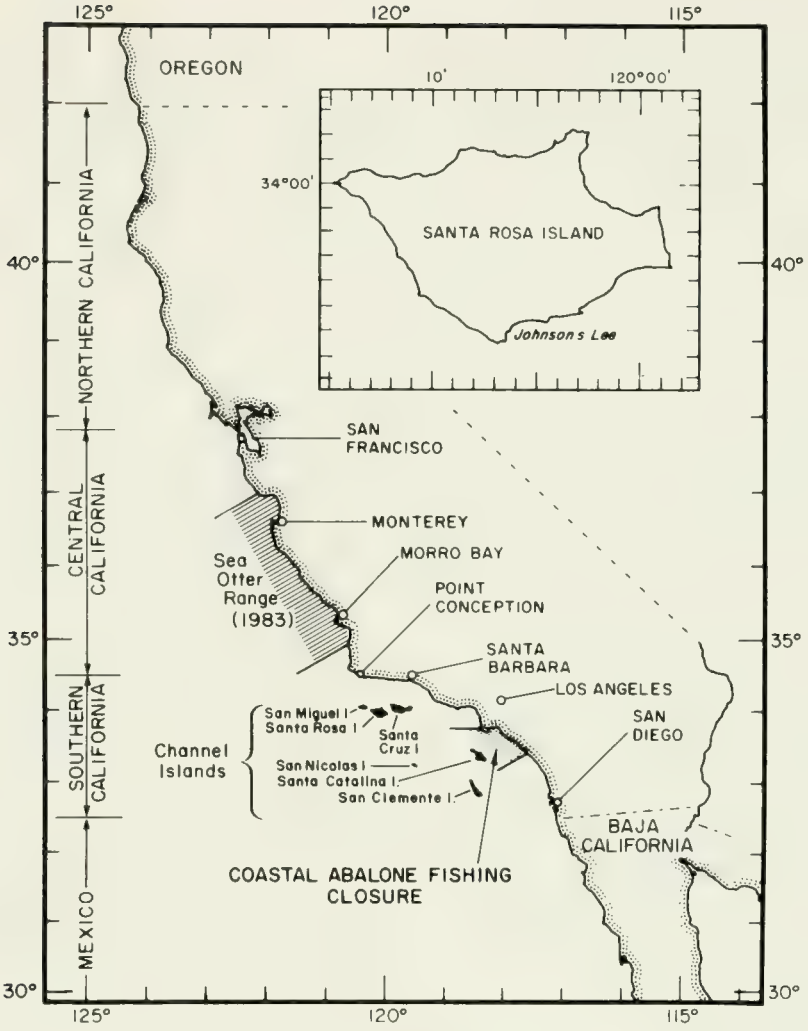

FIGURE 1.—Map of California illustrating the study site and other locations described in the text.

tinued into the late 1980s (Tegner 1989). Several possible causes of the decline have been identified (Burge et al. 1975; Cicin-Sain et al. 1977; Tegner 1989) including sea otter predation in central California, mortality caused by removing and replacing sublegal abalones, environmental changes, inappropriate size limits, and failure of larval recruitment. The last is frequently invoked as a problem in abalone fisheries (e.g., Harrison 1986). Furthermore, because of the central California origin of the red abalone fishery (Cox 1962), little is known about the life history of this species in southern California. Warmer temperatures, different current patterns, and changes in food availability relative to central California are likely to affect population parameters important to the management of the fishery.

To provide a better basis for management of the fishery and for the evaluation of seeding experiments, the University of California Sea Grant College Program and the California Department of Fish and Game (CDFG) conducted a joint study of red abalones at Johnsons Lee on Santa Rosa Island. The site was visited annually during the second week of July from 1978 through 1982 and in June 1984. During the first four visits, 2,145 animals were tagged for growth studies (Haaker et al. 1986); these data were used to calculate the von Bertalanffy growth parameters (Haaker et al. in prep.).

Here we report the results of five years of population studies conducted concurrently with the tagging studies. The objectives were to assess the rates of settlement of young-of-the-year abalones and to follow changes in size-frequency distributions and densities of animals above and below the recreational and commercial fishery minimum size limits. Predator densities and empty shells were used to study predation patterns.

We then use results of the joint study to evaluate the appropriateness of the present size limit for red abalones in southern California. Yield-per-recruit analyses have been commonly used to evaluate size limits and levels of fishing mortality for abalones (e.g., Isibasi and Kojima 1979; Harrison 1983, 1986, Sluczanowski 1984, 1986; Clavier and Richard 1985; Breen 1986). Sluczanowski (1984, 1986), however, showed that egg production from a cohort of females could be reduced to a very small fraction of egg production from an unfished cohort at size limits and fishing rates that seemed reasonable in yield-per-recruit analyses. He suggested that size limits and fishing rates should be examined in the light of both yield- and egg-per-recruit analyses. This approach was used by Breen (1986) for northern abalones, *H. kamtschatkana*, in British Columbia. Egg-per-recruit analyses have also been used widely in assessing size limits for the American lobster, *Homarus americanus*, fishery (Saila and Flowers 1966; Campbell 1985; Ennis 1985).

In this study, we use growth estimates and size-frequency distributions to estimate the natural mortality rate of red abalones, using the method of Fournier and Breen (1983). The mortality and growth estimates are then employed in a yield-per-recruit analysis, using the method of Beverton and Holt (Ricker 1975); and with fecundity data in an egg-per-recruit analysis described below. Results of the egg- and yield-per-recruit analyses are examined together, and implications for management of the red abalone fishery are described. A similar analysis is carried out for pink abalones using data from Tutschulte (1976) and Doi et al. (1977) to consider the generality of the results.

MATERIALS AND METHODS

Field Studies

Johnsons Lee is located on the south coast of Santa Rosa Island (lat. 33°54′N, long. 120°06′W). It is protected from the prevailing northwesterly wind and swell typical of summer but is open to the south and east. In part because of this protection, Johnsons Lee is frequented by both sport and commercial fishermen. The *Macrocystis pyrifera* canopy was generally about a kilometer wide by two or more kilometers in length during this study. The substrate consisted of rocky reefs separated by a network of sand channels. The vertical relief was quite variable but ledges, crevices, and rock piles provided extensive abalone habitat. *Macrocystis* and several species of foliose reds were the most abundant algae; other common plants included *Pterygophora californica*, *Egregia menziesii*, *Laminaria farlowii*, *L. setchellii*, *Desmarestia* spp., *Cystoseira*, spp., articulated and encrusting coralline algae, *Codium fragile*, *Ulva* sp., *Phyllospadix* sp., and *Zostera marina*. Drift algae were abundant.

The 300 × 1,200 m study site was located with its long axis parallel to shore and divided in half by a line perpendicular to shore; the goal was to divide effort evenly between the two areas. The transect protocol was adapted from a previous CDFG study of red abalones at Point Estero (Ebert et al. in prep.) so that the results would be directly comparable. Sampling strategy was based on the method of simple random sampling. Randomly selected transect origins were located with the use of buoys marking corners of the study areas and compass headings to terrestrial topographic features. Transects were tied to the skiff anchor and laid on a 60° compass course paralleling the shoreline and depth contours. Transect depths varied from 7 to 16 m. Bat rays, *Myliobatis californica*, and California sheephead, *Semicossyphus pulcher*, were counted as the line was laid and horizontal visibility was estimated to calculate the density of these predators. The 30 m transects were divided into eight quadrats, each 7.5 × 2 m. Habitat was graded as sand (<25% rock), rock/sand (<75% rock), and rock (>75% rock). Transects that fell on habitat which was greater than 50% sand were not sampled; alternate locations had been preselected. Benthic predators were counted, all abalones visible without disrupting the substrate or the use of an underwater light ("emergent" abalones) were measured, and algae and sea urchins were noted by species and graded as sparse, common, or abundant in each quadrat. Two randomly selected quadrats were destructively sampled. Red (*Strongylocentrotus franciscanus*) and purple (*S. purpuratus*) sea urchins and kelps were counted, all urchins were moved to expose juvenile abalones under their spine canopies, and all rocks turned to locate non-emergent abalones. All abalone shells were collected for measurement and description of shell damage. Transect sample sizes were limited by manpower in 1978 and winds in 1979. To augment shell sample

sizes, all shells encountered in the tagging area (contained within the study site) were measured from 1980 on. Because of the low number of abalones recovered in the random quadrats in 1981, additional quadrats were selected to increase the sample size for the mortality analysis. A sixth visit was conducted in June 1984 to assess the effects of the strong El Niño of 1982–84 (Tegner and Dayton 1987) on the growth of the tagged abalones; shells were also collected at this time.

Mortality Rate

Total mortality rate was estimated from the length-frequency data using the method of Fournier and Breen (1983; Breen and Fournier 1984). For each year, observed numbers in each 3 mm length interval were converted to proportions of the total sample, then multiplied by the density in the destruct quadrats. Observations were then summed for all years 1978–82, and then multiplied by 100 as numbers were so small. The Fournier and Breen method simultaneously estimates the mean lengths-at-age, the standard deviations of lengths-at-age around their mean, the variance of mean lengths around a von Bertalanffy growth curve, the three von Bertalanffy growth parameters (t_0, asymptotic length L_∞, and Brody coefficient K), total instantaneous mortality rate Z, the population proportions-at-age, and the variance of proportions-at-age around a smooth exponential decay curve. Some of these estimates can be fixed or constrained so that existing knowledge is used in obtaining estimates. The number of age classes and various initial conditions must be specified.

Fournier and Breen (1983) used this method to estimate natural mortality rate by sampling abalones in unfished populations. In the population described here, we can estimate only total mortality rate because the population has been subjected to exploitation. The natural mortality rate must be less than this estimate. The minimum legal size for the commercial fishery is close to the average maximum size, and because this method estimates average

TABLE 1.—Parameter values and initial conditions used in estimating mortality rates of red abalones, and their rationale. Parameters without good rationale were varied (see Table 6) to determine the sensitivity of the estimate.

	Value	Rationale
Parameter		
Number of age classes, *NK*	Varied, 12–16	Growth curve; 16 is the maximum number handled by the program
Age of first fully sampled cohort, *NFULL*	Varied, 1–4	Growth curve, sampling considerations
Lower bound on *K*	0.269	Tagging results (Haaker text fn. 3)
Permitted variance of means around von Bertalanffy curve and population proportions around smooth curve	1.0	No reason to force any other result
Lower bound on the first SD	Varied, 7.5, 1.0	Inspection of Figure 3
Upper bound on the first SD	Varied, 8.5, 10.5, 15.5	Inspection of Figure 3
Lower bound on the last SD	Varied, 7.5, 1.0	Inspection of Figure 3
Upper bound on the last SD	Varied, 8.5, 10.5, 15.5	Inspection of Figure 3
Bounds on population proportions	0.0, 1.0	No constraints used
Bounds on mean lengths-at-age	0–300, ages 2 to *NK*-1	Last mean constrained to force estimate of L_∞ of 201 mm per tagging results (Haaker text fn. 3)
Initial conditions		
K	0.271	Based on tagging results
First mean length	30 mm	Based on tagging results, inspection of Figure 3
Last mean length	199 mm at age 16, adjusted slightly for choice of *NK*	Based on tagging results
First SD	8.0	Inspection of Figure 3
Last SD	8.1	Inspection of Figure 3

total mortality rate over most of the size and age range, we believe that the method gives an estimate of the total mortality rate which is not much greater than the natural mortality rate.

Initial values and bounds, and their rationales, are shown in Table 1. We forced the estimation procedure to produce estimates of growth rate parameters consistent with the tagging results from Johnsons Lee (P. Haaker[3]). The lower bound on K was set at 0.269, resulting in an estimated K equal to this; and the last mean length was constrained so as to obtain an estimated L_∞ of 201 mm. Bounds on the standard deviations of lengths-at-age around their means were based on inspection of the length-frequency data (Figs. 2, 3).

[3]P. L. Haaker, California Department of Fish and Game, 330 Golden Shore, Long Beach, CA 90802, pers. commun. 1986.

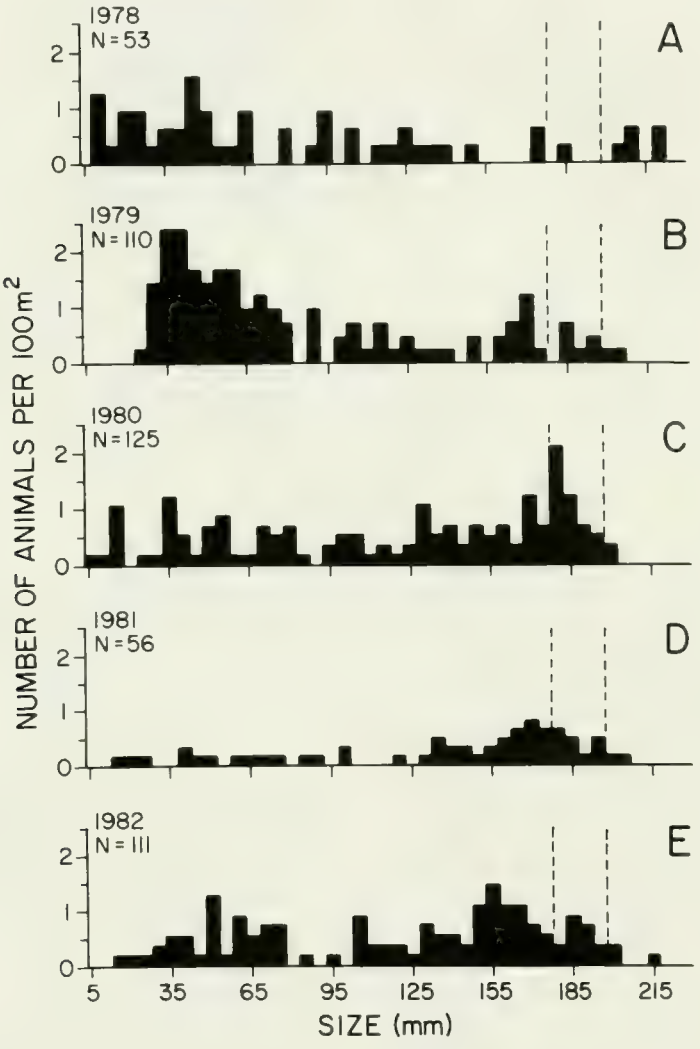

FIGURE 2.—Size-frequency distributions of red abalones recovered in the destruct quadrats by year, 1978–82. The data were scaled for differences in effort between years as follows. Each 5 mm size category for each year was divided by the respective total number of animals found for that year and then multiplied by the density for that year to yield a density at each 5 mm size category for that year. As the resulting numbers are small, each entry was multiplied by 100. The dashed lines indicate sport (178 mm) and commercial (197 mm) legal minimum sizes.

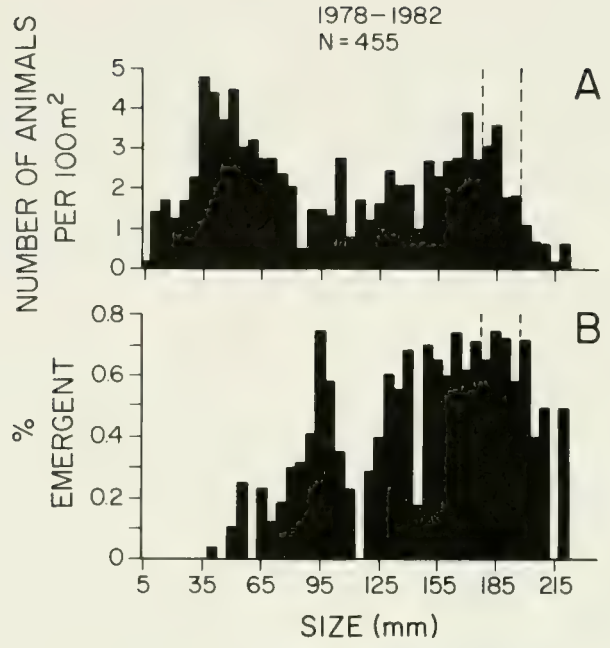

FIGURE 3.—Size-frequency distribution of red abalones found in the destruct quadrats summed for 1978–82. The scaled data from Figure 2 were summed across each 5 mm size category (A). Proportion of the total number of abalones found in the destruct quadrats which were emergent, visible to a diver without turning rocks or the use of a light, as a function of size class. These data were also scaled for differences in effort between years (B). The dashed lines indicate sport (178 mm) and commercial (197 mm) legal minimum sizes.

Yield-Per-Recruit Analysis

A program was written to calculate yield-per-recruit from equation 10.20 of Ricker (1975). Asymptotic weight W_∞ was set to 1,500 g, based on length-weight data collected from Johnsons Lee in 1974 (CDFG, unpubl. data), and an L_∞ of 201 mm. Maximum age λ was arbitrarily set to 25. K was set to 0.269, based on the tagging results (Haaker fn. 3). Two values of natural mortality rate M were used: 0.10 and 0.15, based on the results of this study.

To obtain isopleth diagrams, the instantaneous fishing mortality rate F was varied systematically from 0.0 to 2.0. The minimum size at first capture was varied from 140 to 200 mm.

Yield estimates were also made for pink abalones. Doi et al. (1977) reported growth parameters for males and females from two sites. We used the values for females from Cedros: L_∞ = 186.0 mm, K = 0.233, and t_0 = 0.096. These authors estimate that M = 0.35 at that site. We used this value and also M = 0.20 based on the estimated survival curve from Tutschulte (1976, p. 250). W_∞ was set at 1,216 g, based on the biometric data of Doi et al. (1977). Minimum size was varied from 100 to 180 mm, and F from 0.0 to 2.0.

Fecundity

Egg-per-recruit analysis requires knowledge or an estimate of the way that average fecundity varies with length. Because the procedure compares egg production under specified conditions with egg production in the unfished condition, the absolute number of eggs is not required; only the form of the relation is important.

Four sets of red abalone fecundity data were examined. These were Giorgi and DeMartini (1977), two sets from Ault (1982, 1985), and a set furnished by E. E. Ebert[4]. The first set of data in Ault (1982, 1985) was from a field collection; the second was from laboratory-conditioned animals.

[4]E. E. Ebert, Marine Culture Laboratory, California Department of Fish and Game, Monterey, CA 93940, pers. commun. 1986.

Table 2 shows the regression constants from the predictive regression of the natural logarithm of fecundity on the natural logarithm of length for each data set, and the range of lengths encompassed by each data set. Because the methods were widely different among the various sets and because the absolute numbers of eggs were not considered important, the four sets were combined in the following way. Each data set was scaled by dividing the observed number of eggs by 1 million times the number of eggs predicted for a length of 125 mm, from Table 2. The length 125 mm was chosen because it was most nearly common to all four data sets. The constant 1 million was used to minimize distortion when taking natural logarithms of the scaled data. Then the predictive regression of the natural logarithm of fecundity on the natural logarithm of length was calculated using data from all four sets. The constants obtained are also shown in Table 2.

The validity of this procedure was tested by using the egg-per-recruit model described below and comparing results from each of the fecundity regressions in Table 2. Results obtained using $M = 0.15$, $F = 1.0$ and 2.0, and minimum legal sizes of 179 and 191 mm are also shown in Table 2. The low variation between estimates using different fecundity relations, and the general similarity of the isopleths, allowed us to conclude that egg-per-recruit analysis was not sensitive to our treatment of the fecundity data.

Egg-Per-Recruit Analysis

In egg-per-recruit modelling, one wishes to compare the egg production of a fished population with that of the equilibrium virgin population. The model described here is a simple, deterministic, age-structured model that allows individual variability in length around mean length-at-age. Thus cohorts can be partially recruited to the fishery.

The unfished population is considered first. The number of females of a particular size within a cohort of an unfished population is represented as $NV_{t,j}$, where t indexes cohort age and j indexes length. Each length h_j lies within one of the J intervals

$$(h_j - w/2,\ h_j + w/2); \qquad j = 1, J$$

where $h_j = h_1 + (j - 1)w$ is the midpoint of the jth interval and each interval has width w. If N_0 is the abundance of females at age zero, the female abundance of each cohort in the unfished population is

$$NV_{t,.} = N_0 \exp(-Mt) \qquad (1)$$

TABLE 2.—Fecundity analysis.

Predictive linear regression constants for equations relating fecundity to length in the four data sets described in the text. The equations are

$$\ln(\text{fecundity}) = a + b \ln(\text{length})$$

where length is in mm. The final set of constants describes the equation for the combined data - see text for the method used.

Data set	Range of lengths	a	b	n
Ault (1982, 1985) field-conditioned	112–194	−12.991	5.329	22
Ault (1982, 1985) lab-conditioned	65–182	−6.555	4.283	13
Ebert (text fn. 4)	42–83	−3.482	3.722	11
Giorgi and DeMartini (1977)	134–199	−16.572	6.1557	25
Combined data		−7.672	4.518	71

Results of egg-per-recruit modelling using the regression estimates above. Natural mortality rate was set to $M = 0.15$. Fishing mortality rate F and minimum legal size (MLS) were varied as shown. Results are expressed as percentages of egg production in the virgin population.

	$F = 1.0$		$F = 2.0$	
Data set	MLS = 179	MLS = 191	MLS = 179	MLS = 191
Ault (1982, 1985) field-conditioned	44.5	71.0	41.9	69.5
Ault (1982, 1985) lab-conditioned	48.9	73.8	46.5	72.5
Ebert (text fn. 4)	51.7	75.5	49.3	72.2
Giorgi and DeMartini (1977)	41.3	68.7	38.6	67.2
Combined data	47.9	73.1	45.4	71.8

where M is the instantaneous natural mortality rate. (The dot subscript indicates a summation over all j, i.e.,

$$NV_{t,\cdot} = \sum_{j=1}^{J} NV_{t,j}$$

and similarly

$$NV_{\cdot,j} = \sum_{t=1}^{\lambda} NV_{t,j}$$

where λ is the maximum age attained.) The mean length-at-age L_t can be described by the von Bertalannfy growth curve:

$$L_t = L_\infty \{1 - \exp[-K(t - t_0)]\}. \quad (2)$$

It is assumed that lengths-at-age are normally distributed around their mean, and that standard deviations vary with age in the manner proposed by Fournier and Breen (1983):

$$SD_t = a + b\sqrt{t} \quad (3)$$

where a and b are constants. If lengths-at-age are normally distributed around their mean in the unfished population, the probability that an individual in cohort t will be found in length interval j is

$$Q_{t,j} = \frac{1}{SD_t \sqrt{2\pi}} \int_{h_j}^{h_{j+1}} \exp[-(h - L_t)^2/2\ SD_t^2]\ dh. \quad (4)$$

This was evaluated numerically.

Equations (2) to (4) could be used to describe a continuous growth process. For computational tractability, this model evaluates these relations only at integer values of t. This is equivalent to assuming that growth occurs yearly in one instantaneous increment; or alternatively that all fishing mortality occurs instantaneously when t assumes an integer value.

The number of individuals in all cohorts of the unfished population in length interval j is

$$NV_{\cdot,j} = \sum_{t=1}^{\lambda} Q_{t,j}\, NV_{t,\cdot}. \quad (5)$$

Length-specific fecundity can be described by

$$f_j = c\, h_j^d \quad (6)$$

where c and d are regression constants and f_j is the number of eggs produced by a female of length h_j. If spawning is assumed to occur once annually when t assumes an integer value, total egg production by an equilibrium population of females not subjected to fishing is described by

$$E_{\max} = \sum_{j=m}^{J} NV_{\cdot,j} f_j \quad (7)$$

where h_m is the length at first maturity. $E_{\max}$ is calculated with appropriate parameter values and with a fixed arbitrary value for N_0.

The model is now extended to include fishing mortality acting on all individuals whose length is equal to or greater than a minimum legal size h_R. The number of individuals at a particular size and age in the fished population will be denoted by $N_{t,j}$. It is assumed that no individuals are recruited to the fishery before age 1, so that

$$N_{1,\cdot} = N_0 \exp(-M). \quad (8)$$

In this and all subsequent cohorts, the number of individuals less than legal size will be the same as in the virgin population and can be determined as follows. The proportion of prerecruits in the virgin population is given by

$$QPR_t = \frac{1}{SD_t \sqrt{2\pi}} \int_0^{h_R} \exp -[(h - L_t)^2/2\ SD_t^2]\ dh. \quad (9)$$

The number of prerecruits in each cohort is thus

$$NPR_{t,\cdot} = QPR_t\, NV_{t,\cdot} \quad (10)$$

and the number of individuals exposed to the fishery is

$$NR_{t,\cdot} = N_{t,\cdot} - NPR_{t,\cdot}. \quad (11)$$

The overall survival rate of this cohort over one year will be determined by natural mortality acting on the prerecruits, and by both natural and fishing mortality on the recruits:

$$S_t = [(NPR_{t,\cdot}/N_{t,\cdot}) \exp[-M]] + [(NR_{t,\cdot}/N_{t,\cdot}) \exp[-(F + M)]] \quad (12)$$

Beginning with cohort 1, the abundance of successive cohorts can be determined:

$$N_{t,.} = N_{t-1,.} S_{t-1}. \quad (13)$$

The number of individuals in any cohort t and length interval j can now be determined if a further assumption is made. It is assumed that the length distribution of all recruited individuals within a cohort t is a truncated normal distribution, whose mean is L_t as described by Equation (2). In reality, the recruited segment of an older cohort will comprise several groups of individuals, each group having been exposed to fishing for a different length of time. Thus the length distribution of recruits in a cohort is unlikely to be normal. However, it is not possible to specify their distribution without specifying how varying annual length increments are distributed among individuals in a cohort. This is complex and requires further assumptions, so instead we have made the simplifying assumption described. We believe that the results are not sensitive to this assumption.

The number of individuals in each cohort t and each length interval j is given by

$$N_{t,j} = NV_{t,j} \qquad j < R \quad (14)$$

$$N_{t,j} = Q_{t,j} NR_{t,.}/(1 - QPR_t) \qquad j \geq R$$

and total annual egg production is

$$E = \sum_{t=1}^{\lambda} \sum_{j=m}^{J} N_{t,j} f_j. \quad (15)$$

Initial trials showed that this model is not unduly sensitive to the choice of a and b in Equation (3). The model was run with the same growth parameters used in the yield-per-recruit analysis; $\lambda = 25$; a and b in Equation (3) were set at 8.0 and 0.025 based on inspection of Figure 3; c and d in Equation (6) from the combined analysis in Table 2; and h_f was set to 50. It is assumed that male and female growth rates are the same. This may not necessarily be the case (Doi et al. 1977; Shepherd and Hearn 1983), but we have no information on sexual differences in growth of red abalones. F, M, and the minimum legal size h_R were all varied in the same way as in the yield-per-recruit analysis.

Egg-per-recruit analyses were also made for pink abalones, using the same growth data from females used in the yield-per-recruit analysis. The fecundity relation was obtained from Tutschulte (1976). It was assumed that the number of eggs is proportional to weight (2,078 eggs per gram whole weight in mature females); and that weight is proportional to length:

$$\text{weight (g)} = 2.66 \times 10^{-5} \text{ length (mm)}^{3.24}.$$

Lamda was set at 25; in the absence of data, a and b in Equation (3) were set to the same values as for red abalones; M was set at 0.2; and minimum size and F were varied as for yield-per-recruit analysis.

Simultaneous Analysis

Results from the yield- and egg-per-recruit analyses were combined in a third analysis to examine the relative performance of each combination of minimum size and fishing mortality rate (Breen 1986). Results from each of the previous two analyses are rescaled and then simply multiplied together:

$$SV = (Y/Y\max)\, EPV \quad (16)$$

where SV is the "strategy value" of a particular combination of minimum size and fishing mortality rate, and takes values from 0 to 100; Y is the yield-per-recruit at that combination; $Y\max$ is the maximum yield-per-recruit; and EPV is transformed value of egg-per-recruit, given by

$$EPV = 0.0 \qquad E < 20.0 \quad (17)$$

$$EPV = (3.333\, E) - 66.6667 \qquad 20.0 < E < 50.0$$

$$EPV = 100.0 \qquad E > 50.0$$

where E is the egg production at that combination, expressed as a percentage of the egg production in the unfished situation. The relation of Equation (17) is designed so that when egg production is less than 20% of the virgin egg production, SV is zero; when E is greater than 50% of virgin egg production, SV is equal to the scaled value of yield-per-recruit. The values 20% and 50% are chosen as the values below which most managers would consider egg production to be dangerously low and above which egg production is probably adequate to maintain the stock, respectively.

This analysis was also carried out for pink abalones.

RESULTS

Field Studies

Population Structure

The size-frequency distributions of red abalones recovered in the destructively sampled quadrats

from 1978 through 1982 are illustrated in Figure 2. The size-frequency distributions are significantly different (G test, $P < 0.001$). By inspection, it is apparent that 1978 and 1979 are dominated by smaller animals. The best year for settlement (defined as young-of-the-year or ⩽31 mm) was 1978 (Table 3), when the settlement rate was about three times the average of the other four years. These animals form a prominent mode in 1979 but the mode is not distinguishable in 1980.

the method of Pennington (1983). Assuming no changes in density between years, all data were combined with appropriate weighting for sample size differences to generate average densities of 0.179 m^{-2} (SE ⩽ 0.066) for the total number of abalones, 0.027 m^{-2} (SE ⩽ 0.013) for sport minimum legal sized, and 0.005 m^{-2} (SE ⩽ 0.0035) for commercial minimum legal-sized animals. Due to unestimable correlation between annual data, standard errors are given in terms of an upper bound. Despite intensification of the red sea urchin fishery during

TABLE 3.—Results from the destructively sampled quadrats, 1978–82.

	1978	1979	1980	1981	1982
Number of m^2 sampled	330	360	600	630	570
Red abalones					
Average density (m^{-2})	0.164	0.265	0.217	0.086	0.197
Standard error	0.049	0.161	0.065	0.032	0.049
Young of the year ⩽31 mm) abalones					
Average density (m^{-2})	0.036	0.019	0.017	0.005	0.011
Standard error	0.019	0.010	0.010	0.004	0.006
Percent total population	22.6	6.4	8.0	5.4	5.4
Sport-legal (⩾178 mm) abalones					
Average density (m^{-2})	0.018	0.022	0.045	0.020	0.026
Standard error	0.009	0.014	0.021	0.008	0.009
Percent sport legal	11.3	7.3	21.6	21.4	14.4
Commercial-legal (⩾197 mm) abalones					
Average density (m^{-2})	0.015	0.003	0.002	0.003	0.004
Standard error	0.009	0.003	0.002	0.002	0.003
Percent commercial legal	9.4	0.9	0.8	3.6	2.7
Red sea urchins					
Average density (m^{-2})	2.612	1.836	2.107	1.830	2.868
Standard error	0.780	0.406	0.616	0.667	0.537
Purple sea urchins					
Average density (m^{-2})	0.655	3.536	5.440	4.465	7.830
Standard error	0.177	1.767	1.300	1.407	1.400

The densities of different size categories of red abalones and of red and purple sea urchins in the destruct quadrats for 1978 through 1982 are presented in Table 3. There were no significant changes in the densities of the total number of abalones, young-of-the-year, sport legal minimum (⩾178 mm), or commercial legal minimum (⩾197 mm) sized animals based on 95% confidence intervals around the mean densities. Unequal sample sizes between years and the large number of quadrats with no abalones precluded analysis by ANOVA or the Kruskal-Wallis test. By separating those quadrats that contained abalones from those in which no animals were found, a conditional distribution for the nonzero valued samples could be proposed and tested. Several tests of normality did not reject the hypothesis that the natural log of the nonzero values is normally distributed. Annual total average densities and their variances were then estimated by

this period (Kato and Schroeter 1985), there was no change in red sea urchin density (Kruskal-Wallis test, $0.05 < P < 0.01$). In contrast, there was a significant increase in purple urchin density (Kurskal-Wallis test, $P < 0.001$).

Abalones occupy different microhabitats as their length increases (Cox 1962; Shepherd 1973, Tegner and Butler 1989), and microhabitat selection affects vulnerability to fishing (Witherspoon 1975). The proportion of emergent abalones from the destruct quadrats (1978–82 pooled, $n = 455$) is plotted in Figure 3 as a function of size class. There is an increase in percent emergent with increasing size which appears to level off at about 150 mm and 70% emergent and then decline as the animals attain legal size and emergent animals are apparently fished. Thus a substantial proportion of the largest animals in the population remain cryptic. Nevertheless, the low proportion of the population constituted

by animals of commercial legal size or larger (Fig. 2, Table 3) suggests that fishing pressure is very intense and that fishermen are searching for cryptic abalones. Thirty-five percent of the total number of abalones in the destruct quadrats were emergent (yearly range: 25–50%).

Total, sport-legal, and commercial-legal densities of emergent abalones were calculated from the combined results of the destruct and nondestructively sampled quadrats. Again inspection of the 95% confidence intervals around the yearly means suggests that there were no significant changes in density over the five years studied despite the fourfold larger sample sizes and correspondingly smaller standard errors. The mean density of the total number of abalones from these quadrats was 30% of the mean total density determined from the destruct quadrats, comparable to the 35% of the destruct quadrat animals which were emergent. The density of emergent, commercial legal-sized animals ranged from one to three per 1,000 m^2, again suggesting that Johnsons Lee is intensely searched. In contrast, the density of emergent sport legal-sized red abalones ranged from 10 to 23 per 1,000 m^2. The size-frequency distribution of emergent abalones from both the destruct and nondestruct quadrats is illustrated in Figure 4.

The high variance in the density estimates can be ascribed to two factors. First, a substantial proportion of the rocky substrate was a very flat, pavement-like surface often covered with a thin layer of silt. This surface supports *Macrocystis* and rarely large red abalones, but not small or intermediate-sized animals. Second, the distribution of abalones at Johnsons Lee was highly contagious in all years sampled. The variance to mean ratio was calculated as an index of dispersion and the significance of departures from unity tested with χ^2, and for large samples ($n > 31$), with the normal variable (Elliot 1971). In each case the χ^2 value was highly significant ($P < 0.005$). In 1979, for example, 63% of the total number of abalones found in the destruct samples were in one quadrat.

Habitat Considerations

Cox (1962) reported that abalones prefer areas where there is sand, and Shepherd (1973) recognized the importance of sand patches and channels as areas for the movement and accumulation of algal drift. A χ^2 analysis was conducted to determine whether red abalones were concentrated in the rock/sand areas or uniformly distributed between the rock and rock/sand habitat types (Table 4). On the scale of the 15 m^2 quadrats, red abalones, both emergent and nonemergent, did not show a preference for either habitat type. In contrast, both red and purple sea urchins were found in habitat classified as rock more often than expected.

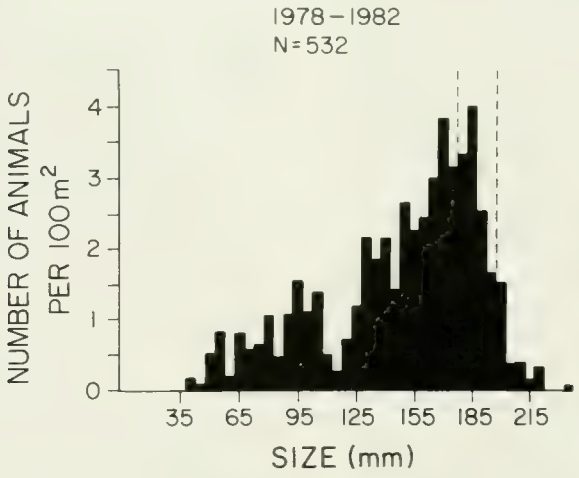

FIGURE 4.—Size-frequency distribution of emergent red abalones found in the destruct and nondestruct quadrats, 1978–82. The data were scaled for differences in effort between years. The dashed lines indicate sport (178 mm) and commercial (197 mm) legal minimum sizes.

TABLE 4.—Habitat analysis. The distribution of red abalones and red and purple sea urchins between rock and rock/sand habitats are tested against the null hypothesis that the animals are uniformly distributed between these two habitat types. Data are pooled for 1978–82.

Destruct quadrats

Habitat sampled	Number of m^2 sampled	Percent
Rock	1,095	45.6
Rock/sand	1,305	54.4

	Emergent red abalones	χ^2 analysis	Non-emergent red abalones	χ^2 analysis
Rock	73	0.051	135	0.003
Rock/sand	84	n.s.	160	n.s.

	Red sea urchins	χ^2 analysis	Purple sea urchins	χ^2 analysis
Rock	3,116	285	6,766	937
Rock/sand	2,357	**	4,519	**

Non-destruct quadrats

Habitats sampled	Number of m^2 sampled	Percent
Rock	2,715	42.9
Rock/sand	3,615	57.1

	Emergent red abalones	χ^2 analysis
Rock	168	0.001
Rock/sand	223	n.s.

** = significant at α = 0.001.
n.s. = not significant.

Predator Populations

We censused all known or suspected macroscopic abalone predators (O'Connell 1953; Pilson and Taylor 1961; Cox 1962; Burge et al. 1975; Tutschulte 1976; Ambrose 1984; Hines and Pearse 1982; Tegner and Butler 1985, 1989) on the transects; the results are presented in Table 5. The most abundant predators were sea stars. Of the suite of species encountered at Johnsons Lee, only two are known to feed on healthy abalones. Breen (1980) reported that *Pycnopodia helianthoides* occasionally fed on *H. kamtschatkana*, and D. Parker[5] observed a *Pycnopodia* eating two juvenile (38 and 46 mm) red abalones at Johnsons Lee in 1977. Schiel and Welden (1987) recently reported observations of *Pycnopodia* predation on juvenile red abalones in the laboratory.

[5]D. O. Parker, California Department of Fish and Game, 330 Golden Shore, Long Beach, CA 90802, pers. commun. 1986.

TABLE 5.—Predator densities for 1978–82.

Predator	Number per hectare (SD) for the year				
	1978	1979	1980	1981	1982
Pycnopodia helianthoides	250 (433)	83 (118)	112 (130)	107 (145)	83 (92)
Astrometis sertulifera	17 (35)	—	17 (51)	4 (18)	—
Cancer spp.	—	42 (56)	42 (69)	12 (30)	26 (79)
Octopus spp.	8 (25)	21 (52)	38 (57)	4 (18)	9 (26)
Scorpanichthys marmoratus	—	—	12 (30)	4 (18)	9 (38)
Semicossyphus pulcher	34 (96)	30 (41)	55 (55)	45 (54)	58 (53)

Astrometis sertulifera consumed abalones up to 80 mm in aquaria experiments (Tegner and Butler 1989). Night dives indicated that the *Pycnopodia* densities in Table 5 are considerably underestimated; juveniles are cryptic during the day. *Astrometis* also tends to be nocturnal or at least crepuscular (MacGinitie and MacGinitie 1968; Tegner pers. obs.). Because many small, empty abalone shells were found without any shell damage, and because juvenile *Pycnopodia* and *Astrometis* are common in cryptic habitats where juvenile abalones live, we suspect that these starfishes may be important predators of small haliotids. *Pycnopodia* and *Pisaster giganteus* both attacked recently replanted adult abalones from the tagging study but *Pisaster* does not appear to be a predator of unstressed abalones (Feder 1959, 1963; Tegner and Butler 1989).

In a study of the gut contents of 87 sheephead collected near San Diego, we found that molluscs are an important part of the diet of smaller fishes and found a juvenile red abalone (15 mm) in one gut (Tegner unpub. data). Thus sheephead predation on unstressed and undisturbed animals is probably rare, but these fishes are attracted to divers and probably take juvenile abalones under the spine canopies of red urchins as the urchins are fished. Sheephead and bat rays do attack recently replanted abalones (Burge et al. 1975; Tegner pers. obs.).

Some predators characteristic of the warmer areas of the southern California Bight were rare or absent at Johnsons Lee. Bat rays, which feed primarily on emergent adult abalones (Tegner and Butler 1989), were attracted to transects on two occasions in 1978 and once in 1981 after the fish had been counted. Spiny lobsters, *Panulirus interruptus*, and sheep crabs, *Loxorhynchus grandis*, have been observed to prey on juvenile and mid-sized red abalones on the Palos Verdes Peninsula (Tegner and Butler 1985). No lobsters and only one sheep crab was seen during the 5 yr course of this study. As all of our visits took place during June and July, we would not have observed any seasonal variation in predator populations.

Patterns of Shell Production

The size-frequency distributions of red abalone shells from 1980 to 1982 and 1984 are illustrated in Figure 5. If we assume a constant rate of mortality independent of age (Fournier and Breen 1983), then we would expect a decline in the frequency of shells with increasing size above the size range where shells are likely to be destroyed by predators. Large modes from about 170 to 195 mm especially in 1980 and 1981 do not fit that expectation. These modes almost certainly reflect bar cut mortality, fatal injuries to abalone soft tissues caused by the collecting tool (Burge et al. 1975; Tegner 1989). In 1981 and 1982, this increase in shell frequency can be resolved into two modes: one just below sport minimum size (178 mm) and one immediately below commercial minimum size (197 mm). The larger number of shells found in 1980 represents years of accumulation; this was the first year in which the tagging area was sampled.

The large shell collections of 1980–82 were examined for evidence of cause of death. Some kinds of shell damage could be ascribed to specific predator types (Cox 1962; Hines and Pearse 1982; Tegner and Butler 1985, 1989) or to the boring sponge *Cliona celata* (Cox 1962; Abbott and Haderlie 1980). Other shells were undamaged or the damage was ambiguous and probably sometimes the result of deterioration after death; for these animals the cause of death was unknown. Fifty-three shells (including data from 1984) had *Octopus* spp. drill holes but, as these cephalopods do not drill all their prey (Tutshulte 1976; Ambrose 1984), this is a minimal estimate of the importance of octopus predation to this abalone population. Red abalones appear to attain a refuge in size (shell thickness) from octopus predation; only three of the drilled shells were larger than 125 mm (Fig. 6). The most common pattern of shell damage was the scratches, chipped edges, and small breaks along the growth edge characteristic of rock crab (primarily *Cancer antennarius* but may include *C. productus*) predation (Cox 1962). Rock crabs appear to be able to handle the full size range of red abalones at Johnsons Lee. *Cliona* was found in a wide size range of red abalone shells but only in very large shells did the degree of infestation appear sufficient to have contributed to the abalones' death by weakening the shells (Cox 1962). The size-frequency distributions of the mortalities attributed to octopuses, rock crabs, and *Cliona* are significantly different from each other (Kolomogorov-Smirnov tests, $P < 0.01$). Bat ray predation can be recognized from shells fractured into large pieces (Tegner and Butler 1989). A small number of mortalities (7–10 per year) could be ascribed to this predator. No shells were found with the acid-etched appearance characteristic of cabezon, *Scorpaenichthys marmoratus*, predation (Hines and Pearse 1982). For the years 1980–82 (tagging area only, $n = 986$), octopuses account for a minimum of about 4% of the mortalities, rock crabs 21%, *Cliona* infestation 6%, and bat rays 2%, and 67% of the deaths could not be assigned on the

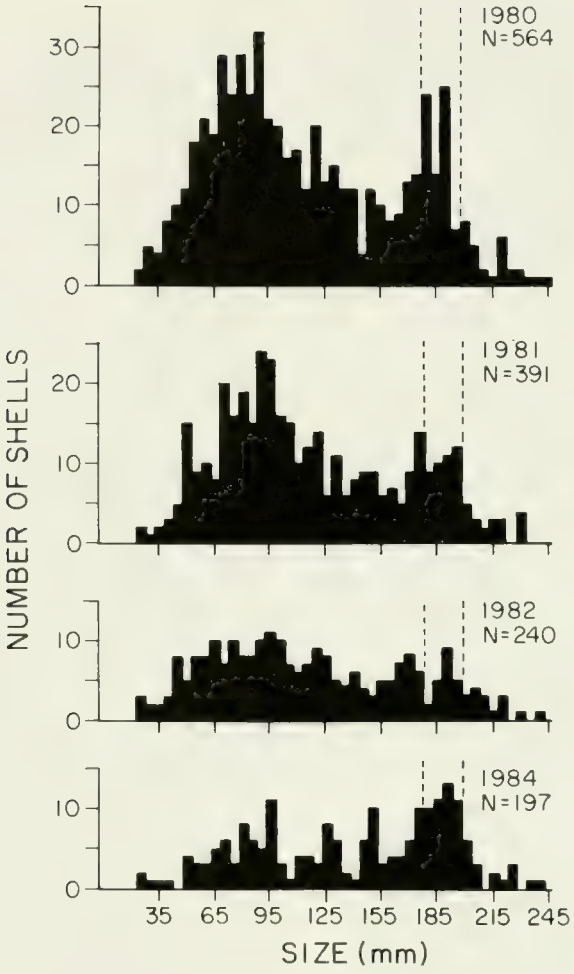

FIGURE 5.—Size-frequency distributions of red abalone shells recovered in the tagging area by year, 1980–82 and 1984. The dashed lines indicate sport (178 mm) and commercial (197 mm) legal minimum sizes.

basis of shell damage. Inspection of the size-frequency distributions of the shells for 1980–82 (Fig. 5) suggests that a minimum of about 10% of the total mortalities during this period can be ascribed to bar cut injuries.

Mortality Rate

Using the values shown in Table 1, total mortality rate Z estimates ranged from 0.165 to 0.222. Sensitivity of the estimate to initial conditions and parameters was tested over a broad range of values; the results from some of these tests are shown in Table 6. The estimate was fairly robust to changes in the assumed number of age classes, increasing as the number of age classes increased. Tagging results suggest that 15 years are required on average for red abalones at Johnsons Lee to reach 200 mm (P. Haaker fn. 3), so we favor estimates based on 16 age classes. Forcing the method to give an estimated L_∞ consistent with the tagging results had little effect. The estimate was sensitive to constraints on the standard deviations of length, increasing as larger standard deviations were permitted. Removing the first two age classes from the estimation led to decreased estimates, but removing further age classes indicated a robust estimate near 0.180. We conclude that the best estimate of total mortality, based on realistic constraints, is $Z = 0.180$.

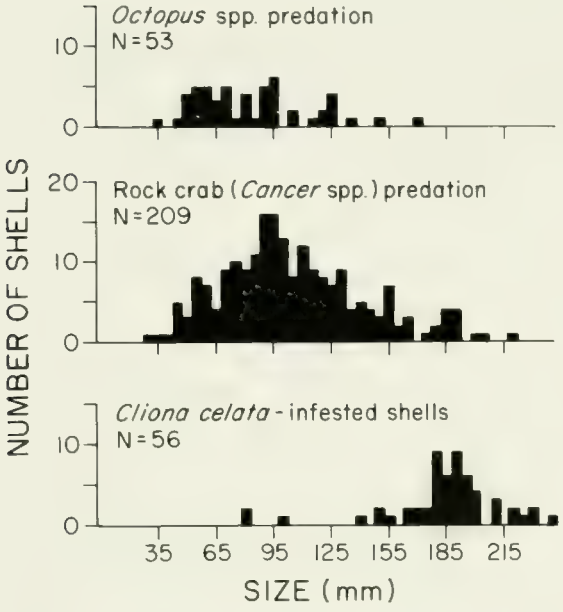

FIGURE 6.—Size-frequency distributions of red abalone shells recovered in the tagging area 1980–82 which could be attributed to a specific predator.

Natural mortality rate must be less than the estimated Z. Commercial exploitation begins at 197 mm, recreational exploitation at 178 mm, and mortality associated with exploitation (bar-cutting) reduces the number of individuals smaller than legal size (Fig. 5). The method used here suggests a value of M around 0.15.

Yield-Per-Recruit Analysis

Isopleth diagrams for red abalones using $M = 0.10$ and 0.15 are shown in Figure 7A and B respectively. The minimum size associated with the maximum yield-per-recruit estimate is sensitive to the value of M used: it is 176 mm when $M = 0.10$, and 164 mm when $M = 0.15$. Both sets of estimates show the pattern described by Breen (1986): except at very low values of F, the yield estimates are not sensitive to variation in F; conversely at low values of F, the yield estimates are insensitive to variation in minimum size.

For pink abalones, yield isopleths are shown in Figure 7C and D. The minimum size producing the greatest estimated yield is very sensitive to the estimate of M. If $M = 0.35$, as Doi et al. (1977) suggested, then the best minimum size is 116 mm; if

TABLE 6.—Effect of changing input parameters and initial conditions on estimated total mortality rate Z in red abalones, using the data in Figure 3 and Table 1. T is the value of the objective function; the goal is to minimize this function in conjunction with realistic mortality rate estimates. Unless specified, bounds in the first and last standard deviations of lengths-at-age for the first and last cohorts are 7.5 and 8.5.

Effect of varying the total number of age classes

NK	16	15	14	13	12
Z	0.196	0.194	0.193	0.182	0.165
T	481	483	486	492	500

Effect of releasing constraints on estimated mean length of the last age class

	Constrained	Unconstrained
Z	0.196	0.195
T	481	481

Effect of changing upper and lower bounds on the estimated standard deviations of lengths-at-age around the mean length-at-age. Bounds on the first line are those for the first cohort; those on the second line are for the last cohort. The asterisk indicates when the model was not actually constrained by the bound.

Bounds	7.5, 10.5 7.5, 10.5	7.5, 15.5 7.5, 15.5	1.0, 15.5 1.0, 15.5*
Z	0.203	0.222	0.222
T	332	236	236

Effect of varying the age of the first age class, *NFULL*, included in the calculation of total mortality rate (*NK* = 16)

NFULL	1	2	3	4	5	6	7
Z	0.206	0.196	0.180	0.180	0.177	0.181	0.174
T	481	481	480	480	480	480	480

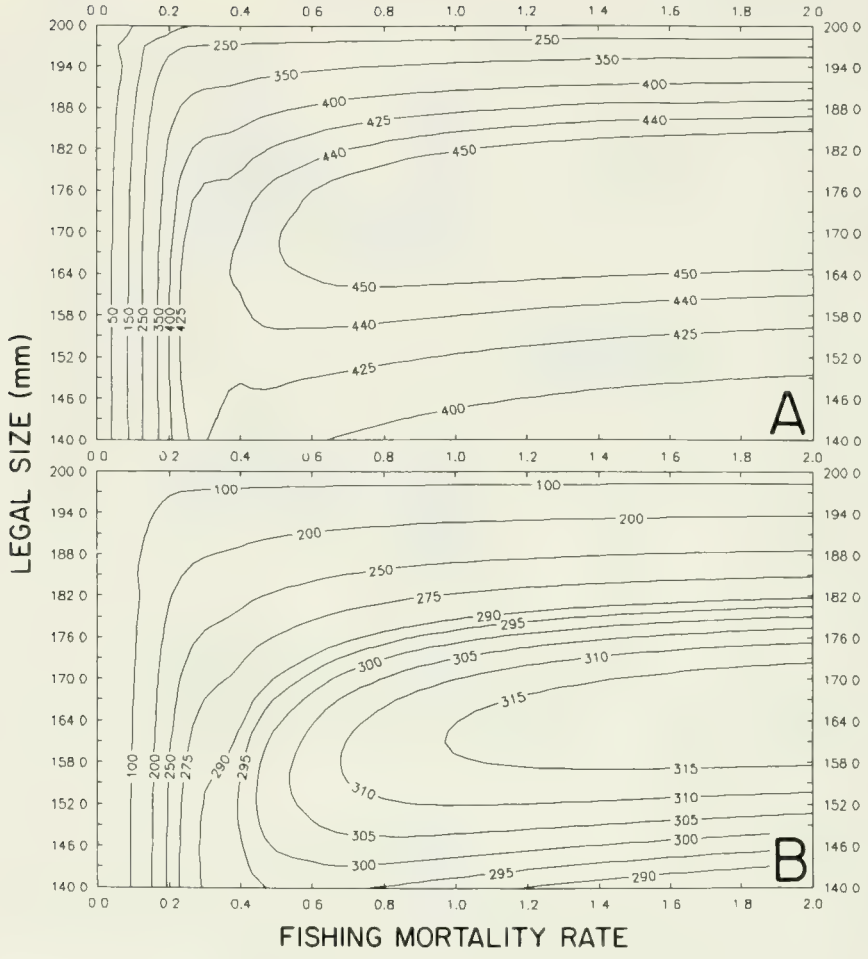

FIGURE 7.—Yield-per-recruit (g) as a function of minimum legal size and instantaneous fishing mortality rate, determined by the method of Beverton and Holt (Ricker 1975). For red abalones, parameters were $K = 0.269$, $L_\infty = 201$ mm, $W_\infty = 1{,}500$ g, and $M = 0.10$ (A) and $M = 0.15$ (B).

$M = 0.20$, then the best minimum size is 140 mm. Both are substantially lower than the present minimum legal size.

Fecundity

Regression constants for the power curves relating fecundity to shell length in the four data sets are shown in Table 2. This table also shows the constants from the combined analysis, which were used in egg-per-recruit analysis.

Egg-Per-Recruit Analysis

Results for red abalones using $M = 0.10$ and $M = 0.15$ are shown in Figure 8A and B respectively. Three points should be noted. First, egg production estimates are sensitive to the natural mortality rate, decreasing as M decreases. Second, even at the smaller recreational size limit and very high rates of fishing, egg production estimates are reasonably high. With $M = 0.10$, egg production by abalones below the recreational size limit should be more than 35% of the virgin population egg production. At higher values of M, large size limits, or lower fishing intensities, the estimate is higher. At the more realistic point of using $M = 0.15$, $F = 1.0$, and the recreational size limit, egg production would be 48%. Third, combinations of F and size limits that produce the best yield-per-recruit lead to

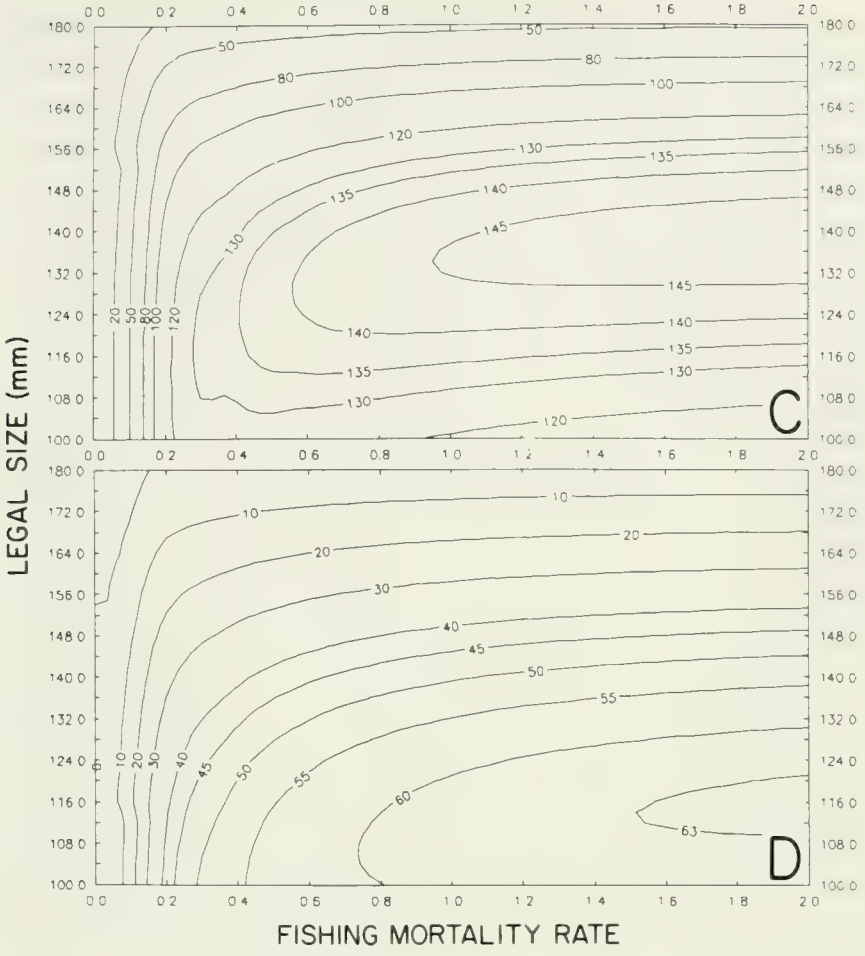

FIGURE 7.—*Continued*—For pink abalones, parameters were K = 0.233, L_∞ = 186 mm, W_∞ = 1,216 g, and J = 0.20 (C) and M = 0.35 (D).

35% egg production at M = 0.10 and 27% at M = 0.15.

For pink abalones, egg production estimates are shown in Figure 8C and D. At F = 2.0 and the present minimum legal size of 152 mm for recreational harvesters, egg production estimates for M = 0.20 and M = 0.35 were 51% and 75% respectively.

Simultaneous Analysis

For red abalones, isoline diagrams illustrating values of SV are shown in Figure 9A and B, using M = 0.10 and M = 0.15 respectively. The curves connecting best combinations of fishing mortality and minimum legal size are quite similar. The optimum combination occurs at high fishing mortality rates; at a minimum legal size of 188 mm when M = 0.10 and at 182 mm when M = 0.15. Note that when F is greater than 0.3, SV is sensitive to the choice of minimum legal size but not to F; while at low values of F the reverse is true.

Results for pink abalones are shown in Figure 9C and D. With both estimates of M, the optimum SV occurs when F = 2.0; however, the best minimum legal size is very sensitive to estimated M. If M = 0.35, the best minimum legal size is 128 mm; if M = 0.20, the best minimum legal size is 152 mm (the present sport minimum size).

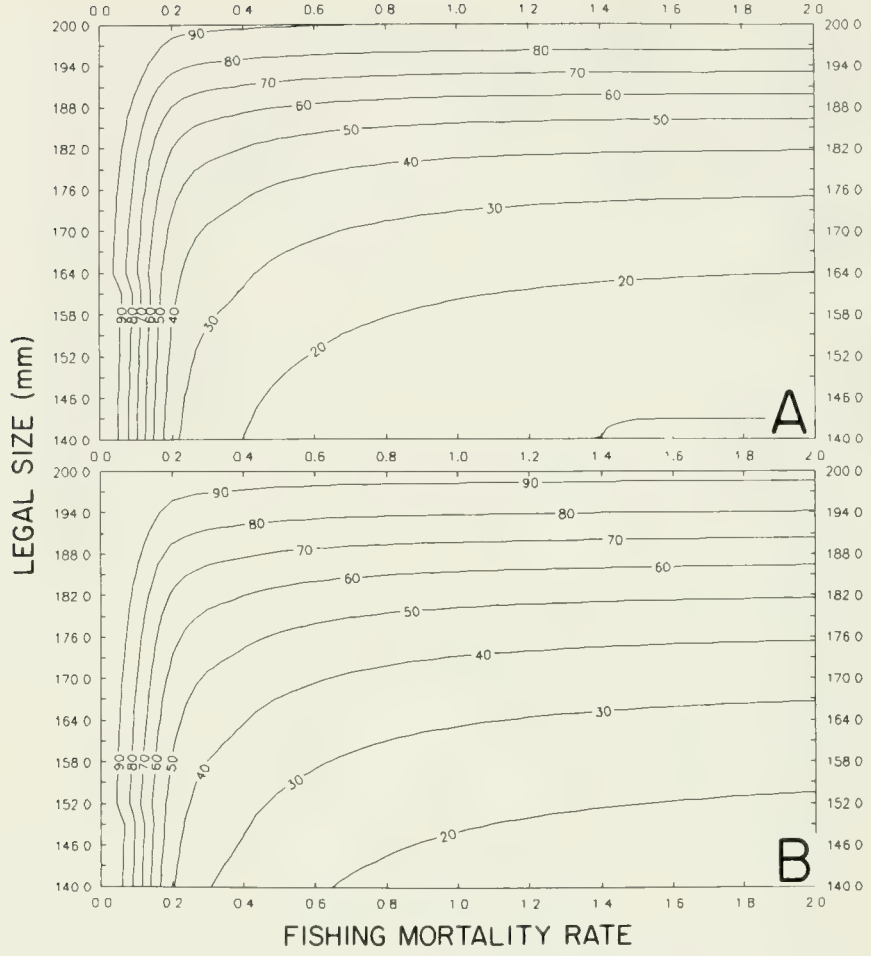

FIGURE 8.—Eggs per recruit, expressed as a percentage of the eggs that would be produced by an

DISCUSSION

Field Studies

Johnsons Lee was a "very good" abalone bed in the late 1940s, an era when strong winds and currents created problems for fishermen with heavy dive gear (Glenn Bickford[6]). More recent assessments suggest that this situation continued; commercial fishermen considered Johnsons Lee to be one of the best red abalone beds in southern California from the early 1970s through 1983. The number of commercial-legal individuals dropped sharply after 1983, perhaps as a result of the El Niño of 1982–84, but the productivity was high again in 1987 (Austin Apodaca[7]). The history of Johnsons Lee cannot be traced beyond this qualitative level; there are no previous quantitative studies and the scale of CDFG block landing records is too large. For the years 1978 through 1982, a period for which our data suggest that the population density was stable, we estimate that the total number of red abalones in our 36 ha study site, assuming an average density of 0.179 abalones per m^2 and that 80% of the habitat was suitable for abalones based on the average transect rejection rate, was 51,552 animals (SE ≤19,008). This included 7,776 (SE ≤3,744) sport minimum legal-sized individuals and 1,440 (SE ≤

[6]G. Bickford, P. O. Box 729, Morrow Bay, CA 93442, pers. commun. 1987.

[7]A. Apodaca, 1702 Mountain, Santa Barbara, CA 93101, pers. commun. 1987.

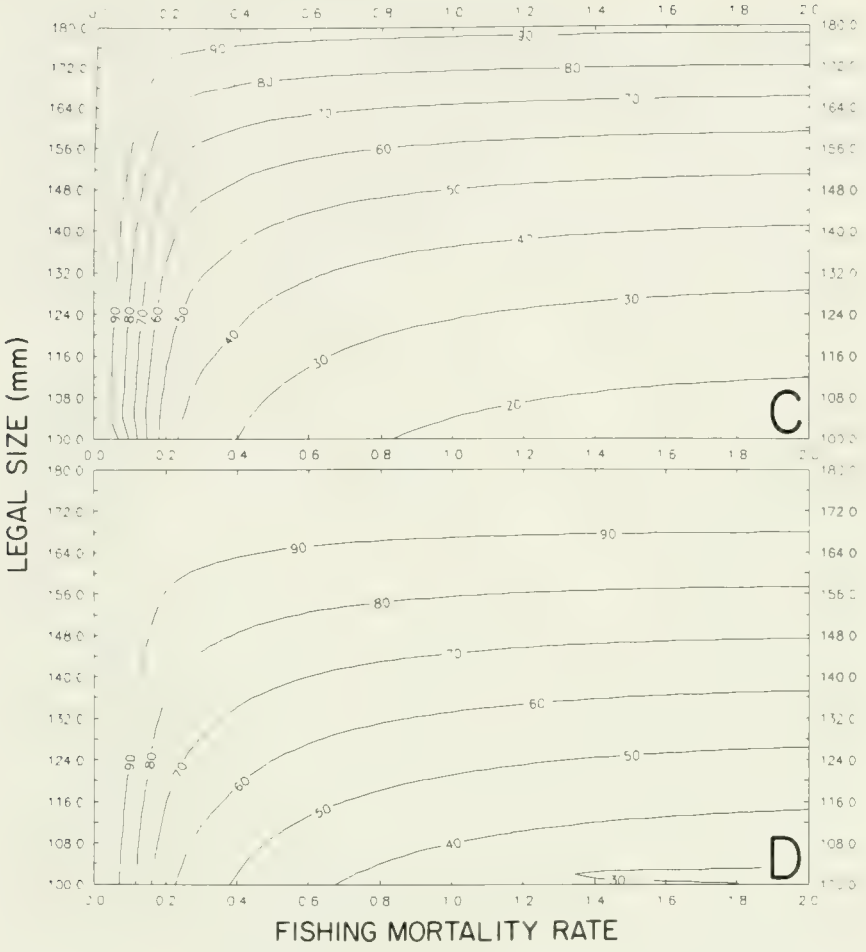

FIGURE 8.—*Continued*—unfished cohort. See text for procedure. Parameters were all identical with those used in Figure 6.

1,008) commercial minimum legal-sized animals. The density of red abalones at Johnsons Lee is comparable to the average 0.2 abalones per m^2 found in the Victorian fishery for *H. rubra* (Beinssen 1979a) but considerably less than recent mean densities of *H. kamtschatkana* in British Columbia (Breen 1986).

Bar cuts have been a continuing problem in California abalone fisheries. Burge et al. (1975) reported market sampling data from 1974, indicating that commercial divers cut 8.6% of their red abalone catch. They felt that the bar cut rate of picked and replaced sublegal animals was likely to be higher because of their more cryptic nature. These authors found a nearly 60% mortality rate in laboratory studies of *H. rufescens* with a 13 mm cut in the foot; mortality is likely to approach 100% in the presence of predators. They presented size-frequency data for pink, *H. corrugata*, and green, *H. fulgens*, abalones which showed decreases in the number of animals within 6 mm of commercial minimum legal size. While the decreases could have been caused by sport harvest or commercial take of sublegal animals, Burge et al. (1975) believed that they were caused largely by the mortality of picked and replaced short abalone. Figures 3A and 4 illustrate similar marked drops in the number of red abalones within 5 mm of both sport and commercial minimum legal size. The size-frequency distributions of shells (Fig. 5) provide strong evidence for mortality of picked and replaced short abalones by sport and especially commercial fishermen. The approximately 10% of total observed mortality which we have attributed to bar cuts is especially damaging to fish-

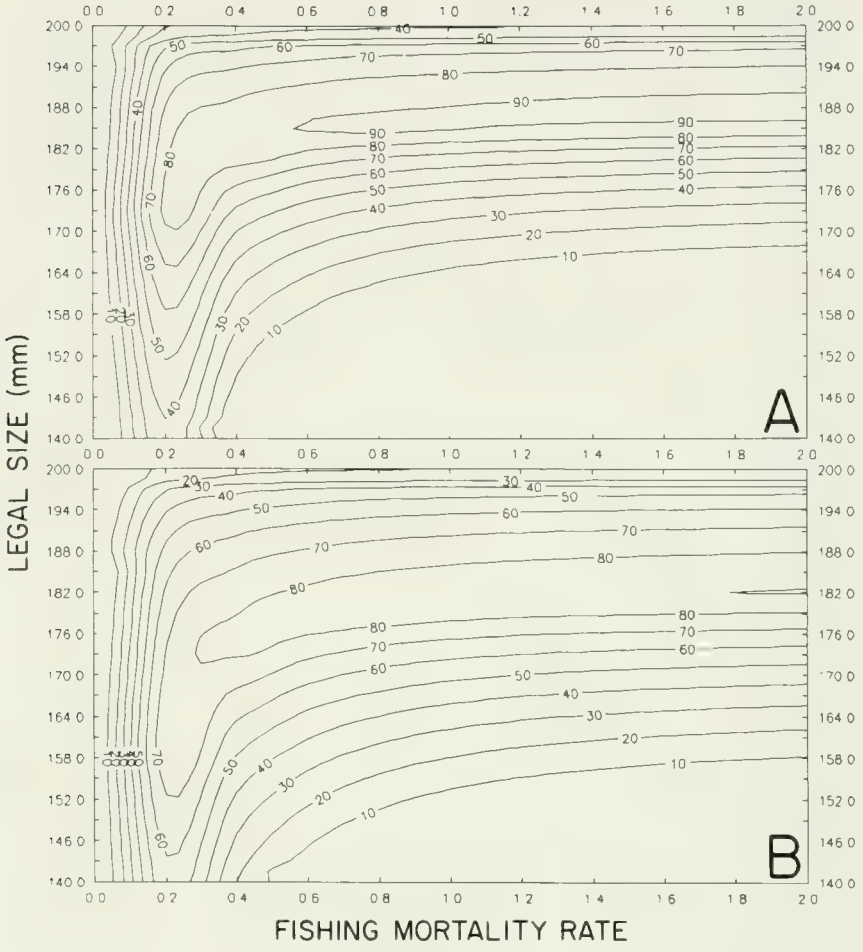

FIGURE 9.—Relative values of various combinations of minimum size limit and fishing mortality rate, using the procedure described in the text and the parameters of Figure 7. Values have a range of

able stocks because animals this size would have a high probability of attaining legal size.

One of the goals of the limited entry legislation, which went into effect in 1977, was to reduce the turnover rate of fishermen; presumably fewer divers with more experience would reduce the frequency with which sublegal abalones are picked and replaced. Similarly, the reduction in the sport daily bag limit in 1976 was accompanied by a requirement that the first four legal-sized abalones taken must be kept; exchange for larger abalones was forbidden (Cicin-Sain et al. 1977). The shell size-frequency data (Fig. 5) clearly indicate that bar cut mortality is continuing in the 1980s. The low density of commercial-legal minimum-sized abalones (Table 3) suggests that bar cuts also reflect intense pressure on a scarce resource; many animals must be picked and measured to sort out the few legal-sized individuals (Burge et al. 1975).

Sea stars are the most abundant of the potential abalone predators at Johnsons Lee, but their role is not clear. A large study of sea star foraging at the Hopkins Marine Life Refuge in central California reported no observations of abalone being eaten by sea stars (Harrold 1981 reported in Hines and Pearse 1982) but *Pycnopodia* is known to have very different diets in different habitats (Mauzy et al. 1968). Montgomery (1967) demonstrated that young (<100 mm) red abalones exhibit strong flight responses to *Pycnopodia* in aquaria experiments. Similarly, Hines and Pearse (1982) observed that contact with *Pycnopodia* caused abalones to rapidly move 5–20 cm deeper into crevices at Hopkins. This behavior, plus the large number of juvenile

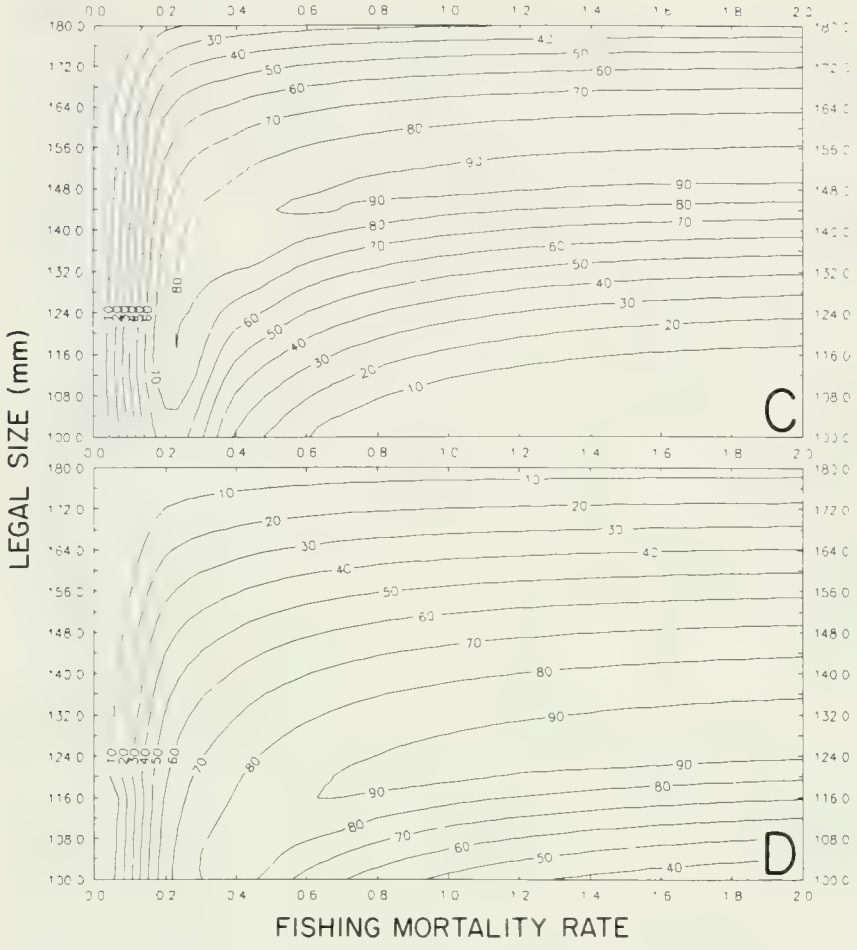

FIGURE 9.—*Continued*—0–100 with 100 representing maximum yield-per-recruit and at least 50% of possible egg production.

abalone shells without any shell damage and the abundance of juvenile *Pycnopodia* and *Astrometis* in cryptic juvenile abalone habitat, leads us to suspect that these sea stars are important predators of small haliotids. Conversely, there is more support for the role of rock crab predation (Cox 1962). The 21% mortality assigned to *Cancer* predation in this study was the largest proportion which could be unambiguously assigned to any predator, and this value is undoubtedly an underestimate of rock crab importance as many cases of minor chipping were considered ambiguous. Given their nocturnal activity pattern and tendency to bury in the sand by day (Ricketts and Calvin 1968), the observed densities of *Cancer* (Table 5) may be considerably underestimated.

The predation patterns observed at Johnsons Lee varied considerably from the results of a study of juvenile (<100 mm) red abalones on the Palos Verdes Peninsula (Tegner and Butler 1985), a mainland site about 160 km southeast of Santa Rosa Island. Here 33% of the shells (n = 325) found in a year-long study had octopus drill holes and 34% were ascribed to crustacean predation, primarily by spiny lobsters. The octopus density at Johnsons Lee is much lower than at Palos Verdes, but these cephalopods may still be important predators of juvenile red abalones; 9 of 21 shells recovered from a small-scale seeding (size range 22–52 mm) experiment conducted at Johnsons Lee in 1977 had been drilled (Tegner unpub. data). The relatively low level of octopus predation at Johnsons Lee may also reflect the larger average size of individual animals at this location; Figure 6 suggests that red abalone attain

a refuge in size from this predator at about 125 mm.

Hines and Pearse (1982) present size-frequency and density data for several red abalone populations in central California under different predation regimes which contrast markedly with the results from Johnsons Lee. The Hopkins Marine Life Refuge has been within the sea otter range for many years and the abalone population is dependent on an extensive crevice refuge. The density of emergent abalones was higher than at Johnsons Lee (0.18 m^{-2} vs. 0.06 m^{-2}) but the effects of intense otter predation are apparent in the population structure; the average size of emergent red abalones was 8 cm (vs. 15 cm at Johnsons Lee) and of shells was 10 cm (vs. 11 cm). At a site north of the otter range, the average size of red abalones was 18 cm, more than twice the size at Hopkins, and an average shell size of 21 cm was found at an intermediate site recently invaded by the mammals (Hines and Pearse 1982). These rather dramatic differences underscore the importance of studying abalone population dynamics in a biogeographic context.

In his monograph on California abalones, Cox (1962) reported that the San Miguel Island fishery produced predominantly red abalones while all the other Channel Islands produced mostly pink abalones. (These were the only two haliotids fished at this time in California.) In this 5 yr study, only three live pink abalones were found on the transects at Johnsons Lee, all in 1978. Unpublished CDFG block landing records for 1983 indicate that the red abalone harvest exceeded the take of pink abalones on Santa Rosa, San Nicolas, and Santa Cruz Islands as well as on San Miguel Island. The reason for this apparent shift in species composition is not clear. Growth and larval survival of *H. rufescens* are optimal in cooler temperatures than for *H. corrugata* (Leighton 1974), but there is no evidence of a cooling trend since the early 1960s sufficient to produce this shift. As both species have been fished actively since the mainland south of Point Conception and the Channel Islands were reopened to commercial harvest in 1943 (Cox 1962), it is unlikely that competition was important. Pink abalones are more susceptible to bar cuts (Burge et al. 1975), a factor which would affect both the yield to the fishery and the reproductive potential of the stocks. The shift may reflect relative differences in egg production or larval dispersal potential. The average red abalone landings for 1981–86 represented 17% of the average landings for this species for 1950–70. For pink abalones, which were not affected by sea otter predation during this time period, this figure was 3%, suggesting that *H. corrugata* is less resilient to fishing pressure.

Mortality Rate

Our mortality rate estimate for *H. rufescens* is higher than Smith's (1972) estimate (an annual turnover rate of 0.05), that was based on a length-frequency sample of large animals in northern California. Our estimate is consistent with the direct observations of survival at Hopkins (Hines and Pearse 1982), but lower than estimates of turnover rate from empty shell production obtained in the same study. These authors favor the estimate based on shell production, considering that their choice of sites for making direct observations may have been biased toward good refuges from predation. Without predation by sea otters, mortality rates in the two studies would appear to be similar.

The Fournier and Breen (1983) method can only estimate total mortality rate, which in this study is based on both exploited and preexploited segments of the population. We estimate natural mortality as being less than this estimate. A second problem is the assumption that each cohort resulted from an initial cohort of the same size. The data (Fig. 2) do not support this assumption but the effects of variable recruitment are minimized by combining data for several years in a standardized form.

Natural mortality rate may vary with age in some molluscs, and such variation is important in making estimates from age-structured models (Appledoorn 1988). Mortality may be higher for the first two age classes of red abalones, because we obtained higher mortality estimates when these were included (Table 6). After the first two age classes mortality estimates were stable, supporting the assumption that natural mortality is independent of age.

Implications for Management

Several authors consider abalones to be particularly susceptible to "recruitment overfishing" sensu Gulland 1973 (e.g., Harrison 1969; Sainsbury 1977; Mottet 1978; Breen 1980). Some reasons for this belief are as follows (see also Harrison 1986). Low adult natural mortality rates lead to dense "top-heavy" populations with a high proportion of large adults. Because fecundity increases exponentially with length, much of the breeding capacity of the population can be concentrated in these large individuals. Diving is an extremely efficient harvesting method on open substrate types (e.g., Beinssen 1979b). Abalones have a high unit value, so economic

self-regulation of the fishery does not occur. Thus the fishery can remove a high fraction of the accumulated stock in a short time (e.g., Kojima et al. 1978), leading to greatly reduced breeding potential and thence recruitment failure. Although this mechanism is an attractive explanation for unexpected declines in exploited abalone populations, Harrison (1986) pointed out that recruitment failure has never been convincingly demonstrated in an abalone fishery. Such a demonstration would be difficult, because the stock-recruit relationship is not known for any abalone species. Without knowing the relation between stock and subsequent recruitment, one canot know how much breeding stock must be maintained. However, egg-per-recruit analysis can provide clues as to whether egg production is adequate (e.g., Sluczanowski 1986; Praeger et al. 1987).

For California red and pink abalones, the decline in fishery landings may have many causes (Burge et al. 1975; Cicin-Sain et al. 1977; Tegner 1989). The declines occurred after large increases in fishing pressure, so one is tempted to conclude that recruitment overfishing as described above was a contributing cause. Our analysis does not support that conclusion, at least for red and pink abalones in southern California. Our egg-per-recruit analyses suggest that, with the present minimum legal sizes, egg production would be maintained at healthy levels for both species, even at very high fishing mortality rates. For red abalones, with our estimate of $M = 0.15$, egg production would be maintained at about 50% even if the population were fished down to the recreational size limit. It is hard to imagine recruitment failure happening at this level of egg production.

We conclude that simple recruitment overfishing is not a satisfactory explanation for the decline in red and pink abalone landings. Some possible qualifications should be noted. First, the results of egg-per-recruit analysis are sensitive to the growth parameters used as input. Underestimation of either L_∞ or the Brody coefficient leads to overestimation of relative egg production. Because growth in abalones varies greatly among habitats (Sainsbury 1982; Shepherd and Hearn 1983; Breen 1986) and varied considerably from year to year in this study (P. Haaker fn. 3), egg production analyses based on growth data from one site might not reflect the situation at other sites. The paucity of published growth data for California abalones, and the importance of such data in assessing the fishery, point to a need for further growth studies.

Second, the mortality caused by handling sublegal abalones (picking and replacing them) has the same effect on egg production as a reduction in minimum legal size. Thus estimates of egg production at the present minimum legal size are known overestimates. However, egg production is still good well below the present legal sizes (Fig. 8C, D) so this problem is unlikely to affect our conclusion.

Third, simple analyses such as this ignore spatial and ecological complexities. At a particular site, fishing mortality might be much higher than the population-wide rate. If dispersion of larvae is limited, as Prince et al. (1987) suggested, locally intense harvesting events could cause long-lasting changes in local populations. Another complexity is that abalones may aggregate to spawn (Shepherd 1986), thus becoming far more vulnerable to fishing mortality than the nonbreeding population. Finally, populations reduced to low densities may not be able to realize their potential egg production because of reduced fertilization efficiency.

Although this study does not support the idea that recruitment overfishing has been a serious problem, it does support the idea that reproductive factors should be considered along with yield estimates when fishing strategies are developed. The strategies which lead to the best yields in red abalones (Fig. 7A, B) are strategies that lead to lower egg production than others (Fig. 8A, B). As Sluczanowski (1984, 1986) found for South Australian abalones, egg production can be greatly increased with small reduction in yield-per-recruit by choosing different combinations of minimum legal size and fishing mortality rate.

If recruitment overfishing cannot be invoked to explain declining landings, what happened? Some of the explanations offered by Burge et al. (1975) may remain valid. Many sublegal abalones may be killed by handling. In at least the early years of the fishery, the stock was being "fished down" as years of accumulated production were removed; the landings may have been higher than sustainable levels during this period. However, it seems unrealistic to argue that the fishing down process lasted from 1950 through 1970 (e.g., Cox 1962). Sea otters have effectively removed abalones from parts of the coast that contributed to the fishery. Fishing closures have eliminated access to other areas.

Direct and indirect environmental effects may also be partly responsible, especially for species near the end of their range, such as pink abalones on the northwestern Channel Islands. Abalones do not necessarily spawn every year (e.g., Sainsbury 1982). Temperature appears to be a major controlling influence on spawning (Pearse 1978; Uki and Kikuchi

1984). Food availability is also involved; when massive storms removed virtually all the kelp from Palos Verdes in the winter of 1983, green abalones missed their normal late spring spawning (Tegner and Dayton 1987). Temperature also effects larval survival (Leighton 1974); thus variability in the reproductive success of abalones could be intimately related to variations in water temperature regimes. Paine (1986) observed that purple sea urchins settled successfully only four times in 20 years on the outer Washington coast and suggested that settling success was associated with warm-water events. Similarly, Tegner and Dayton (1987) found strong settlement of pink abalones into what had been a red abalone bed at Palos Verdes and simultaneously found a near absence of young reds during the 1982–84 El Niño. Shepherd et al. (1985) suggested that poor settlement of *H. scalaris* is associated with cool-water temperatures. Similar suggestions are made by Hayashi (1980) and Forster et al. (1982). Interannual variability in surface currents will have a direct effect on larval transport; larvae which end up in unsuitable habitat are not likely to contribute to fishable stocks. This has been demonstrated for several finfishes (Walford 1938; Nelson et al. 1977; Bailey 1981; Sinclair et al. 1985). The transport anomalies associated wth El Niños (Chelton et al. 1982) may be responsible for purple urchin settlement in Washington and the pink abalone event described above.

An indirect effect of hydrographic events is proposed by Sakai (1962) who found a high correlation between abalone landings and harvests of the seaweed *Undaria pinnatifida*. Sakai suggested that seaweed growth, and consequently abalone production, varies with the strength of the Kurile (Oyashio) Current. Similarly, El Niños in California involve a reduced California Current and increased transport of warmer waters from the south (Chelton et al. 1982). During the major El Niño of 1957–59, Cox (1962) reported that abalone growth practically ceased, body tissues appeared to shrink, gonad development was minimal, and there was poor recruitment to the fishery. When Johnsons Lee was sampled in 1984, few animals were found above sport minimum legal size and growth was the lowest observed during this study (P. Haaker fn. 3). It is now clear that the warm water associated with these events leads, in addition to kelp mortality, to a sharp decrease in the nitrogen content of algal tissues; such kelp is probably an inadequate food to support herbivore growth or reproduction (Tegner and Dayton 1987).

The egg-per-recruit model we used was deterministic, whereas breeding success is stochastic. Future work should try to measure the degree of variation in settlement and recruitment success, then evaluate population responses with a simulation model incorporating the variability observed. Studies of this type have shown that stochastic variation in recruitment creates difficulties in rebuilding depleted stocks (e.g., Archibald et al. 1983). If abalone larval settlement is only occasionally successful, maintenance of the population may require a much larger breeding stock than otherwise expected.

The importance of environmental effects in explaining declining abalone abundance is evident in several studies where abundance or recruitment declined in the absence of a fishery. Breen (1986) and Sloan and Breen (1988) reviewed the evidence for *H. kamtschatkana* in British Columbia. Sainsbury (1982) observed fluctuating recruitment in an unfished population of *H. iris* in New Zealand. In the English Channel Islands, *H. tuberculata* has undergone strong fluctuations in recruitment and abundance, even where not exposed to a fishery (Forster et al. 1982). If unexploited stocks undergo major fluctuations in recruitment caused by environmental effects, then the fluctuations in heavily exploited stocks may be severe under the same conditions. As Gulland (1973) pointed out, "if the fluctuations in year class strength, independent of the abundance of adults, are large, then it is possible that a serious collapse of the stock can occur before the need for management is recognized and appropriate measures taken."

To manage abalones properly, fishery managers would need to know the relation between breeding stock size, which they can manipulate through regulation, and subsequent stock size. If there were little relation, then the best strategy would be to maximize the yield from whatever recruitment occurs. At the other extreme, Prince et al. (1987) suggested a strong relation between local stock size and recruitment. In this case the manager must balance the need to maximize yield with the need to maintain good egg production, and the need to maintain resilience in the face of environmental uncertainty.

In the absence of better information, we suggest that prudent abalone management should follow the lead of Sluczanowski (1984, 1986) and adopt the goal of maintaining egg-per-recruit at the cost of some potential yield. Our results support Harrison's (1986) contention that the minimum size limit should be the basic management tool in meeting this goal, as fishing mortality rate is unlikely ever to fall below $F = 0.3$. To set appropriate size limits requires good information on growth patterns, fecundity and

breeding patterns, and natural mortality rates. Our study underscores the need for better data on California abalone species.

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INTEGRATION OF JAPANESE AND UNITED STATES SABLEFISH MARKETS

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ABSTRACT

As United States sablefish production becomes more tightly interwoven with Japanese markets, the U.S. sablefish fleet could become more vulnerable to changes in Japanese market conditions and government policies, and U.S. policies would have to be formulated with an eye on Japanese conditions. If U.S. ex-vessel and Japanese markets are integrated by prices, then price information transmitted from the Japanese market affects the behavior of the U.S. markets, while in turn, if the markets are not price integrated, U.S. market behavior is independent of price movements in Japan. To assess this likely market integration, this paper examines the price integration of the Pacific coast and Alaska's fixed gear ex-vessel markets and the Tokyo central wholesale market over 1981–1986. The Pacific coast market is found to be segmented from the Tokyo market while a form of price integration exists between the Tokyo and Alaska markets. The paper concludes with a number of implications for policies in both the United States and Japan.

Following the Manguson Fishery Conservation and Management Act (MFCMA) of 1977, United States fishermen have been given an opportunity to replace foreign harvesters of several species as the first link in a chain of supply for some foreign markets. In few fisheries have the results of this industry domestication been more strongly demonstrated than in those for Pacific sablefish. As the Japanese witnessd their harvest in U.S. territorial waters fall from 25,000 to 50,000 thousand metric ton (t) range in the mid-70's to negligible amounts in recent years, U.S. producers expanded their sablefish operations, thereby facilitating greater U.S. exports. Throughout much of the early 1980's, these increases in U.S. exports were accompanied by continued reductions in Japanese harvests.

These factors have combined to increase the ex-vessel sablefish revenue received by Pacific coast and Alaska groundfish fishermen to a level second only to that for Alaska pollock. In contrast to pollock, which is currently harvested predominantly by joint venture operations, sablefish is almost exclusively domestically harvested and processed. The dramatic increase in U.S. production and revenues had coincided with an increase in U.S. sablefish exports to Japan from just 340 t in 1981 to roughly 12,000 t in 1986.

The growing reliance of Japanese sablefish markets on U.S. exports concomitant with an expanding U.S. sablefish fleet suggests the possibility of a growing integration of the Japanese and U.S. ex-vessel sablefish markets. To the extent that U.S. production becomes more tightly interwoven with Japanese markets, the U.S. sablefish fleet will become more vulnerable to changes in Japanese market conditions. Changes in Japanese prices or the exchange rate have a much greater potential for impacting U.S. fishermen today than even 5 or 10 years ago. This possibly increasing integration of U.S. ex-vessel and Japanese sablefish markets by both price and commodity flows and the increased economic dependence on the U.S. export of sablefish for both societies underscores the need for a better understanding of the manner in which these markets are integrated.

This paper empirically examines the integration by prices of U.S. and Japanese sablefish markets over the time period 1981–86. We consider the Tokyo central wholesale (Tsukiji) market and the U.S. ex-vessel markets in Alaska and along the Pacific coast. Because quite a sizable amount of the domestically caught sablefish is retained in the United States, consideration of U.S. markets at some level beyond the ex-vessel might seem desireable, but we restrict our attention to the ex-vessel level because of data availability. We further restrict

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our analysis to the pot and longline, or fixed gear, sector of the fleet, because these vessels produce the higher quality sablefish desired by Japanese consumers.

We consider Tokyo the central wholesale market, because it is playing an increasingly dominant role in the handling of sablefish in Japan. Before the imposition of harvest restrictions, when the Japanese fishing fleet was responsible for providing most of the domestically consumed sablefish, the centralized market in Tokyo played a less important role in the distribution of sablefish; it may have handled less than 50% of that consumed. As Japan was forced to rely increasingly on imports of sablefish, the clearinghouse in Tokyo has become more prominent by providing a conduit for the imported product. Throughout most of the 1980's, the Tokyo market has generally handled 60–70% of the sablefish sold in Japan.

MARKET INTEGRATION AND PRICE ANALYSIS

This section defines market integration and presents the formal models used to empirically assess the structure of any price integration which may exist.

Market Integration

Markets integrated by prices are those markets in which prices do not behave independently. In market economies, market information to the different participating economic agents is largely transmitted by prices, so that an understanding of the manner in which markets are integrated by prices can contribute to the general process of policy formulation. Markets may be integrated by prices to different degrees and along some dimensions but not others. Geographical links or interregional trade are among the most important. Two major issues of these spatial price linkages have been most frequently examined: whether or not markets are integrated by prices, and if so, the extent and nature of this integration.

Regression analysis is the preferred method of assessing market integration. This procedure implicitly assumes that prices of commodities in spatially dispersed markets can independently move in a nonintegrated market system. Changes in weather patterns or government policies affecting the quantity and price of a commodity in a market should not have an impact on prices in other markets when the market system is not integrated by the price mechanism. Price movements across markets would be fundamentally independent, and price movements within markets would reflect local responses to local conditions.

Dynamic Spatial Price Differentials

Ravallion (1986) recently proposed a dynamic model of spatial price differentials from a central market to local markets for a tradeable good. Ravallion's model permits each local price series to have its own dynamic structure, allows for any correlated local seasonality or other characteristics, and provides for an interlinkage with other local markets. Moreover, the alternative hypotheses of integration of markets by price and market segmentation are encompassed within a more general model, thereby allowing for nested statistical testing. Finally, Ravallion's dynamic model distinguishes between the concepts of instantaneous market integration and the less restrictive idea of integration as a long-run target of the short-run dynamic adjustment process. Thus, while short-run adjustment could be statistically rejected by the data, so that trade does not immediately adjust to spatial price differentials, it is still possible to determine if there is any long-run tendency toward market integration.

Ravallion (1986) proposed the following econometric model of a T-period series of prices for N regions:

$$P_{it} = \sum_{j=1}^{J} a_{ij} P_{it-j} + \sum_{j=0}^{J} b_{ij} P_{1t-j} + c_i X_{it} + e_{it}, \quad i = 2,\ldots,N, \qquad (1)$$

where market 1 is the central market (here Tokyo), X_i ($i = 1,2,\ldots,N$) is a matrix of nonprice influences on local markets, the e_{it}'s are appropriate error processes, J is the number of time periods to be lagged, and the a's, b's, and c's are parameters to be estimated.

Several hypotheses about interregional trade and market integration can be formulated as linear parameter restrictions on Equation (1) and tested by F-tests (Ravallion 1986):

Market Segmentation

The null hypothesis of local market segmentation states that changes in the central market prices will have no effect, immediate or lagged, on prices in the ith local market. Market i could be called seg-

mented if

$$b_{ij} = 0, \quad j = 0,1,2,\ldots,J, \tag{2}$$

which can be determined by imposing the parameter restriction of Equation (2) on Equation (1), and testing this restricted model against the unrestricted model of Equation (1) with an F-test. Nonrejection of the linear restrictions or null hypothesis indicates that the price in local market i depends only on its own lagged values and local market characteristics.

Short-Run Market Integration

A price change in the central market will be immediately and fully passed on to the ith local market price if

$$b_{i0} = 1. \tag{3}$$

This hypothesis, in addition, requires that there be no lagged effects on prices in the future:

$$a_{ij} = b_{ij} = 0, \quad j = 1,2,\ldots,J. \tag{4}$$

If both Equations (3) and (4) are accepted as parameter restrictions, then market i is integrated with the central market within one time period.

A weaker form of short-run market integration will also be tested, in which the lagged effects need only vanish on average:

$$\sum_{j=1}^{J} a_{ij} + \sum_{j=1}^{J} b_{ij} = 0. \tag{5}$$

An additional indicator of short-run market integration occurs if $b_{i0} = 1$, but Equation (4) or (5) do not hold (Heytens 1986). In this case, short-run market integration cannot be accepted, yet economic forces causing central market price changes are generally being reflected in the local price level. A form of integration is occurring, even though the central and local markets are not being fully linked in the short run; that is, changes in the price margin between the central and local markets are not being fully passed on.

Absence of Local Market Characteristics

This hypothesis assumes that

$$c_i = 0, \tag{6}$$

where c_i is a vector if there is more than one local market characteristic. Testing this hypothesis is of interest when local prices are suspected to have different seasonality than the central market. In this case, X_{it} can be defined as a matrix of dummy variables.

Long-Run Market Integration

A long-run equilibrium is one in which market prices are constant over time, undisturbed by any local stochastic effects. Thus, when $P_{it} = P_i^*$, $j = 2,\ldots,n$, $P_{1t} = P_1^*$, and $e_{it} = 0$ for all t, Equation (2) takes the form

$$P_i^* = \frac{P_1^* \sum_{j=0}^{J} b_{ij} + X_{it}c_i}{1 - \sum_{j=1}^{J} a_{ij}}. \tag{7}$$

Long-run market integration now requires that

$$\sum_{j=1}^{J} a_{ij} + \sum_{j=0}^{J} b_{ij} = 1. \tag{8}$$

If this linear parameter restriction is not rejected by an F-test, then the short-run process of price adjustment described by the model is consistent with an equilibrium in which a unit increase in the central market price is fully passed on in local market prices. Markets where previous central market prices and past spatial price differentials are the primary determinants of local prices (rather than previous local prices) are well connected in the sense that supply and demand conditions in the central market are communicated effectively to local markets. In the long run, the central market influences local market prices irrespective of previous local conditions, even though traders may fail to connect the two markets through commodity flows in the short run (cf Timmer 1974). Acceptance of the short-run restrictions implies long-run market integration, but the reverse is not necessarily true.

If the linear restriction for long-run market integration is not rejected, then more efficient estimates of the remaining parameters and more powerful statistical tests are possible if the model is reestimated with long-run market integration imposed. Equation (1) under long-run integration can be written in the following equivalent form (Ravallion 1986):

$$P_{it} - P_{it-1} = (a_{it} - 1)(P_{it\ 1} - P_{1t\ 1}) + \sum_{j=2}^{J} a_{ij}(P_{it\ j} - P_{1t\ j})$$

$$+ b_{10}(P_{1t} - P_{1t-1}) + \sum_{j=1}^{J-1} (b_{10} - 1 - \sum_{k=1}^{J} a_{ik} + b_{ik})$$

$$\times (P_{1t-j} - P_{1t-j-1}) + e_i X_{it} + e_{it}. \qquad (9)$$

Changes in local market prices, $P_{it} - P_{it-1}$, are then attributable to changes in central market prices and past spatial price differentials between local and central market prices. The latter variables allow for the possibility that the markets are not observed in an integrated equilibrium at a given time period, so that there is feedback from prior disequilibria.

Ravallion (1986) proposed the following sequence of nested F-tests for the different null hypotheses. First, test for long-run integration. If long-run market integration is not rejected, then it should be imposed on the model with subsequent tests based on a restricted form such as Equation (9). If the null hypothesis of long-run market integration is rejected, then short-run market integration and market segmentation are tested.

Specification Issues

Central and local market prices in Equation (1) might be simultaneously formed. This possibility leads to a simultaneous equation problem, so that parameter estimates could be biased and inconsistent. Ravallion (1986) noted that the simultaneity in the system can be easily dealt with by using an appropriate instrumental variables estimator. This paper uses the two-stage least squares estimate of Equation (1) formed by replacing P_{1t} with its predicted values from the reduced form equation obtained from a regression of P_{1t} against its own values lagged one period, the values of prices in all local markets lagged one period, all dummy variables, and the time trend variable.

Several nonprice influences (X_{it}) are possible. First, the influence of seasonality is accounted for by quarterly dummy variables for winter, spring, summer, and fall. Second, the possibility of long-term effects from increasing U.S. exports coupled with continued reductions in Japanese harvest are captured by a linear time trend. Third, a dummy variable for the years 1984–86 is included to capture any effects from the reduction of Japanese sablefish catch within the U.S. 200 mile zone and concomitant increase in U.S. harvests and exports of sablefish that experienced an important increase beginning in 1984 (Hastie 1988).

Lagged Effects

Any lagged effects in the model are likely to arise from sluggishness in price adjustment, delays in transportation, cold storage inventory holdings, and expectations formation under price uncertainty (Ravallion 1986). A maximum lag of six months was chosen. This relatively long lag length allows for Tokyo's fall prices to influence Alaska's spring prices and ex-vessel markets after Alaska harvesting has tapered off over the winter months.

A 6 mo lag length also accommodates the effects of commodity flows from the Alaska's spring harvests on price formation in the Tokyo market. The peak Alaska harvests occur in late spring and early summer. The major Tokyo wholesale purchases (approximately 65% of the year's total) are concentrated from late May through October. After these purchases, cold storage inventories become particularly important in order to accommodate the major Japanese consumption, which takes place in the fall and winter months. Thus, the major inventory holdings in the marketing chain occur at a higher level than that which our study examines and should not directly affect the model.[3]

U.S. inventory holdings and transportation lags make only a minor contribution to price formation. Sablefish are shipped frozen. Cold storage holdings prior to export are relatively small and declining in

[3]While multicollinearity from current price and six lagged prices could present a problem in estimates and tests of significance for individual regression coefficients, the hypothesis tests in this paper are for the joint effects, requiring tests on the joint confidence region, so that multicollinearity presents far less of problem than it ostensibly might appear.

importance. Beginning in 1984, these inventory holdings were generally 15% of the exports. Before 1984, cold storage holdings formed a greater proportion of exports, because exports were substantially more limited in quantity. Shipping lags are somewhat seasonal, and while no specific information is available, shipments certainly require only a relatively limited time.

Asymmetric Pricing and Price Transmission

When any form of full short-run market integration is absent, price changes in the market of origin are not immediately and fully passed on to the local markets within one time period. Yet, while the central and local markets may not be fully linked by prices in the short run, if markets are not segmented, a weaker form of short-run market integration may still be taking place. Moreover, the short-run response to rising prices emanating from the central market can differ from the response to price declines. This price stickiness produces asymmetric local market price responses to central market price changes.

While the Ravallion market model does not formally incorporate these forms of market integration—incomplete short-run market integration with asymmetric pricing, a modified Wolfram (1971) framework developed by Young (1980) and Ward (1982) does offer a formal model of price formation for examining this possible form of short-run market integration. The modified Wolfram framework presented in Ward uses a finite distributed lag function:

$$P_{it} = a_{0t} + \sum_{j=1}^{J} [b_j'(P_{1t-j+1} - P_{10}) + (b_j'' - b_j') P_{1t-j+1}''] + e_t \quad (10)$$

where P_{10} indicates the central market price in the initial time period and where

$$P_{1t}'' = (P_{1t-i} - P_{1t-i-1}) Z_{t-1}'' \quad (11)$$

where $Z_{t-i}'' = 1$ if $P_{1t-1} < P_{1t-i-1}$

$= 0$ otherwise.

The estimate of $(b_j'' - b_j')$ provides a direct test of the asymmetric condition, where b_j' measures the response to a rising price P_1 and b_j'' relates to a declining price P_1.

Polynomial distributed lags can be substitited into Equation (11) to provide structure, thereby reducing multicollinearity and conserving degrees of freedom. For the case of a second-order polynomial,

$$b_j' = c_0 + c_1 j + c_2 j^2$$

$$\text{and } b_j'' - b_j = d'_0 + d_1 j + d_2 j^2, \quad (12)$$

where the c's and d's are parameters to be econometrically estimated. The values and standard errors of the b's can then be recovered from these estimates of the c's and d's. Significance tests on d_0, d_1, and d_2 as a group (a linear restriction on Equation (10)) provide direct tests of asymmetric price linkages.

DATA

Average monthly market price data for the Tokyo central wholesale market during 1981–86 were obtained from the Tokyo Central Wholesale Market Yearbook. These are implicit prices formed by dividing monthly total revenues by comparable quantities. Most of the sablefish sold in this market are not a homogenous commodity, so that movements of these average sablefish prices may reflect changes in the composition of the product form and quality. However, because we were only able to obtain simple (unweighted) arithmetic average prices formed by linear aggregation, we were forced to assume that different product forms and grades are perfect substitutes for each other. The data are in raw, unseasonalized form, without any prior seasonal adjustments or smoothing (which would otherwise confound the distributed lag relationships).[4]

Alaska and Pacific coast ex-vessel prices tend to be competitively formed. Seattle dominates as the port of export. Many of the prices received by Alaska vessels are formed in a Seattle auction, in which roughly 10–12 processors or brokers bid after the auction has received a call from an Alaska vessel reporting its catch information. Some ex-vessel prices in Alaska and the Pacific coast are directly formed when a vessel lands its catch at a processor.

[4]Because these prices are average implicit prices, they may not be equilibrium prices. Spot prices are available, but a problem with spot prices is that the price of the time and day sampled may not be indicative of the entire month. Also, while spot prices are available for different size classes, proportions in the market mix are unavailable.

Formation of fixed prices and informal contracting occur between some processors and harvesters, but flexibility nonetheless exists in the fixed price negotiated prior to harvesting so that stochastic fluctuations in the size, quality, and composition of landings are accommodated. While wholesalers can be strung out along the coast, seemingly in a strong position to offer noncompetitive prices to vessels, competition is nonetheless stronger than initially appears among wholesalers and processors, and harvesters always have the option to land in different ports if they feel that prices are monopsonistic. In Alaska, approximately 5–7 processors handle the bulk of Alaska's products, although there are at least 50 processors in total. Complete Alaska price data were only available from 1984 through 1986.

Japanese prices were adjusted for inflation by the use of the Japanese Consumer Price Index. Japanese prices were converted to U.S. dollars after adjusting for the yen-dollar exchange rate. Japanese prices were further converted from kilograms to pounds. U.S. prices were adjusted for inflation by the GNP implicit price deflator. Japanese prices are for eastern dressed weights and U.S. prices correspond to round weight, but the empirical results should be unaffected because of a constant adjustment rate between the two product forms.

EMPIRICAL RESULTS

Figure 1 depicts the Tokyo wholesale and the Alaska and Pacific coast ex-vessel sablefish prices by month over the time periods 1984–86 and 1981–86, respectively. All prices are in constant dollars per pound, although as noted above, the Tokyo prices correspond to eastern dressed weight and the U.S. prices correspond to round weight. The figure indicates that the Tokyo wholesale prices are generally more stable than the ex-vessel prices. The

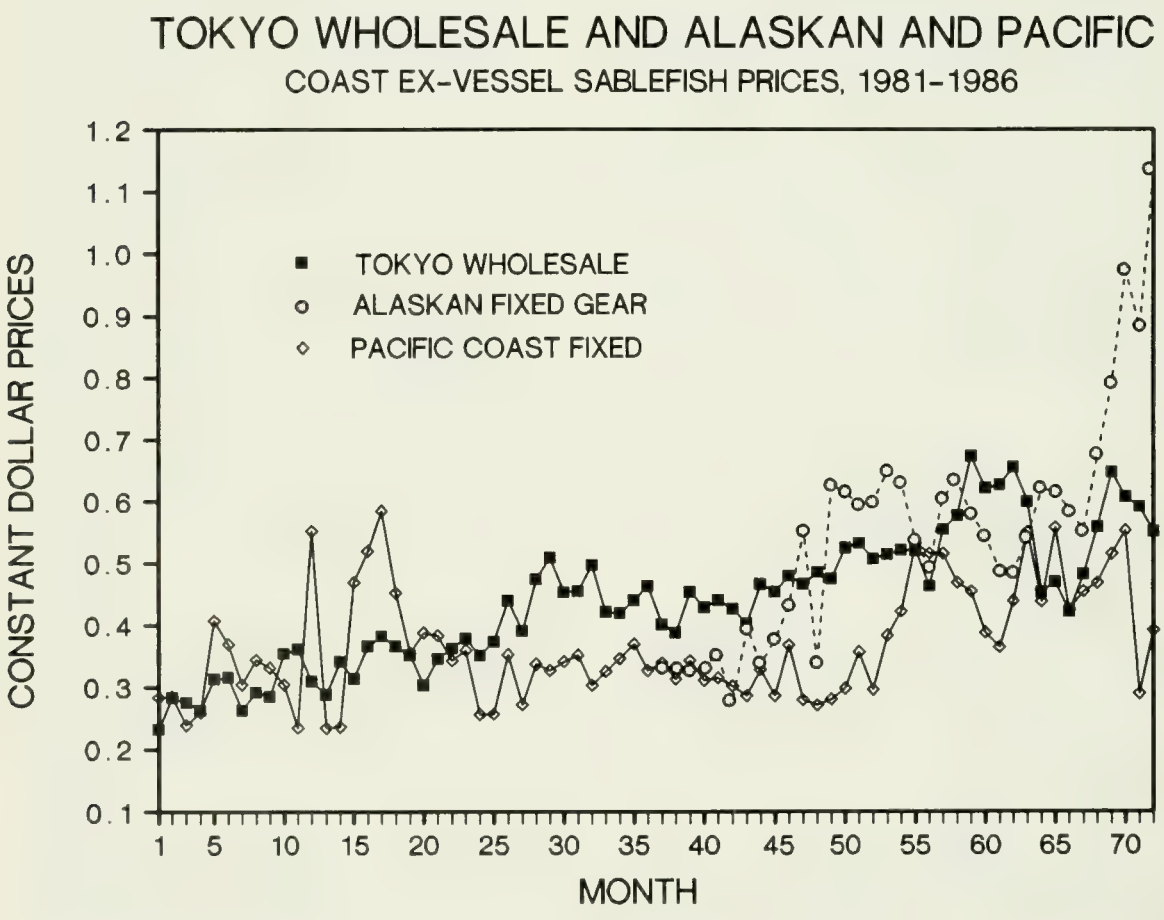

FIGURE 1.—Tokyo wholesale and Alaska and Pacific coast ex-vessel sablefish prices.

Pacific coast ex-vessel prices are also generally lower than the Alaska ex-vessel prices, perhaps reflecting a faster growth rate in market demand for Alaska's fish. An upward trend also exists for all prices. Because the Tokyo prices correspond to eastern dressed weight and correspond to a higher market level, the Tokyo prices can be generally expected to lie above the ex-vessel prices. Interestingly, this relationship only begins some time in 1983, perhaps reflecting the increasing importance of the Tokyo wholesale market as a clearinghouse for the increased imports from the United States and the sharp drop in Japanese harvests that began about this time (so that Tokyo prices now include additional transport, handling, and other market costs). Finally and most importantly, because no simple, direct, one-to-one relationship appears to exist between the Tokyo and U.S. prices, regression analysis can make an essential contribution to understanding the nature of the market integration.

To apply the Ravallion model, we specified the Tokyo wholesale market as the central market and the Pacific coast and Alaska ex-vessel fixed gear markets as the local markets.[5] The unrestricted model given by Equation (1) for six lagged periods ($J = 6$) was estimated by two-stage least squares. The autocorrelation and partial autocorrelation plots for the residuals were reasonably flat for both local markets, indicating the serial correlation does not present a problem. All statistical tests were F-tests for linear restrictions, which were all evaluated at a 5% level of significance. The results from these F-tests are reported in Table 1.

The importance of the local market characteristics was first examined. As indicated in Table 1, the null hypothesis that seasonal dummy variables for Alaska were not important was not rejected at 5%. Also, the linear trend variable was excluded because it did not contribute to the overall explanatory power of the Alaska model. The 1984 dummy variable was omitted from the Alaska model because 1984 was the first year that the Alaska's price series was used in the analysis. The seasonal dummy variables did not contribute in a statistically significant way to the unrestricted model for the Pacific coast, so that the quarterly dummy variables were not included in further regressions. The 1984 dummy variable and linear time trend did not contribute to the overall explanatory power of the unrestricted model for the Pacific coast when taken as a group (but not individually). The linear time trend for the Pacific coast was nonetheless retained in the model because of the clear upward trend in real prices exhibited by the data. The final version of the unrestricted model given in Equation (1) does not have any local market characteristics for Alaska, and only includes a linear time trend for the Pacific coast. The regression results for the final versions of the unrestricted model are reported in Table 2. These final versions of the unrestricted model were then used for the hypothesis tests on the form of market integration.

The next null hypothesis which was tested was that of long-run market integration for Alaska. As indicated in Table 1, it was not rejected at a 5% level of significance. In order to obtain more efficient estimates of the parameters and more powerful statistical tests for the short-run market integration hypothesis test for Alaska, the model was respecified with long-run integration imposed as in Equation (9) and all subsequent tests conducted against this restricted form. (The regression results are available from the authors upon request.) All three

TABLE 1.—Hypothesis tests for the integration of Japanese, Pacific coast, and Alaska sablefish markets. Distributions of F-test statistics given in parentheses of form (numerator degrees of freedom, denominator degrees of freedom).

	Local market	
Null hypothesis	Pacific coast	Alaska
No local seasonality	0.458* (4,47)	3.309 (4,17)
No local time trend and 1984 dummy	1.429* (2,51)	
No local time trend		0.034* (1,22)
Long-run integration	2.870* (1,52)	0.023* (1,23)
Short-run integration		4.230 (12,24)
Short-run integration (weak form)		4.012 (2,24)
Short-run integration (weakest form)		6.621 (1,24)
Market segmentation	0.826* (6,52)	

NOTES: The unrestricted model is Equation (1) for $J = 6$ estimated using two-stage least squares. The table gives F-tests of the linear restrictions on the model implied by each null hypothesis. Short-run integration tests conditional upon maintained hypothesis of long-run integration as given in Equation (9).

* indicates nonrejection of null hypothesis at 5% level of significance

[5]Within-sample, bivariate direct Granger causality tests (see Squires 1986 for a discussion) were first applied to verify if Tokyo is indeed the source of price formulation in the U.S. markets, or whether prices are simultaneously determined between Tokyo and the local markets, or whether price linkages even exist at all. The null hypotheses that prices were first formed in either the Alaska or Pacific coast ex-vessel fixed gear markets were rejected at a 5% level of significance in both instances. The null hypothesis that sablefish prices first formed in the Tokyo wholesale market lead the Pacific coast ex-vessel fixed gear sablefish prices was also rejected, thereby suggesting market segmentation. The null hypothesis that Tokyo prices lead Alaska ex-vessel fixed gear prices was not rejected, indicating some form of sablefish market integration with price leadership most likely coming from Tokyo.

TABLE 2.—Parameter estimates of dynamic model of spatial price differentials for Alaska and Pacific coast fixed gear ex-vessel and Tokyo wholesale sablefish markets. [$t - j$] denotes current time period less j time periods. Standard deviations in parentheses.

Variable	Parameter estimates	
	Alaska	Pacific coast
Time trend		0.131E-4 (0.087E-5)
Ex-vessel price [t − 1]	0.565* (0.272)	0.300* (0.149)
Ex-vessel price [t − 2]	0.381 (0.225)	0.101 (0.157)
Ex-vessel price [t − 3]	0.237 (0.235)	0.130 (0.164)
Ex-vessel price [t − 4]	0.035 (0.227)	0.345 (0.169)
Ex-vessel price [t − 5]	−0.044 (0.253)	0.180 (0.163)
Ex-vessel price [t − 6]	−0.269 (0.240)	−0.154 (0.149)
Tokyo price current	−0.593 (0.673)	−0.268 (0.438)
Tokyo price [t − 1]	0.568 (0.698)	0.255 (0.440)
Tokyo price [t − 2]	0.249 (0.361)	0.080 (0.322)
Tokyo price [t − 3]	0.237 (0.381)	−0.406 (0.314)
Tokyo price]t − 4]	−1.090* (0.359)	0.258 (0.325)
Tokyo price [t − 5]	0.723 (0.422)	−0.037 (0.320)
Tokyo price [t − 6]	−0.055 (0.275)	0.288 (0.288)

NOTE: Two-stage least squares estimates of final version of unrestricted model given by Equation (1).

* denotes statistically significant at 5%.

forms of short-run market integration were rejected for Alaska at a 5% level of significance, as indicated in Table 1.

The null hypothesis of long-run market integration was not rejected for the Pacific coast at a 5% level of significance, as reported in Table 1. However, given that this nonrejection was only marginal, the evidence was only weak for long-run integration. The alternative null hypothesis of market segmentation for the Pacific coast was therefore tested and decisively not rejected; market segmentation is the most likely market relationship.[6]

[6]The results of direct Granger causality tests discussed in footnote 3 further indicated no long-run net price leadership between the Tokyo wholesale and Pacific coast ex-vessel fixed gear markets, thereby reinforcing the conclusion of no market integration by price. Nonetheless, this relationship could have changed over 1987–89.

To summarize, the Tokyo wholesale and Pacific coast ex-vessel fixed gear sablefish markets are likely to be segmented over the period 1981–86. Changes in the Tokyo wholesale market prices will have no effect, immediate or lagged, on the Pacific coast market. Instead, the local market price depends only upon its own lagged values and local market conditions. Pacific coast fixed gear ex-vessel sablefish markets operate independently of the Tokyo central wholesale market. Should the expansion of sablefish export markets be considered important, then the general lack of communication of prices and other market information should be targeted for improvement.

The Tokyo wholesale and Alaska fixed gear ex-vessel sablefish markets are well integrated by prices in the sense of a long-run tendency in the short-run adjustment process. Changes in Alaska ex-vessel sablefish prices can be attributed to changes in Tokyo wholesale prices and past spatial price differentials between the Tokyo and Alaska markets. Supply and demand conditions in the Tokyo central wholesale market are communicated effectively to the Alaska ex-vessel market and influence prices there irrespective of previous local conditions. In fact, previous local prices and localized market conditions contribute little to current Alaska ex-vessel prices. These two markets are well integrated by prices in this manner, although traders may fail to connect the two markets through commodity flows in the short run, particularly during the winter months.

The absence of any form of full short-run market integration for Alaska suggests that a price change in the Tokyo wholesale market is not immediately and fully passed on to the Alaska fixed gear ex-vessel market within one month. Given the important reduction in Alaska fishing during the winter months and the dispersed and often geographically isolated nature of harvesters, processors, and brokers, this result is not surprising. Yet, while the two markets are not fully linked by prices in the short run (one month), a weaker form of short-run market integration may still be taking place due to the economic forces causing Tokyo wholesale market price changes generally to be reflected in the Alaska fixed gear ex-vessel price level.

To examine one possible form of incomplete short-run integration by price between the Alaska and Tokyo markets, the modified Wolfram model was applied. This approach allows for asymmetric price responses in the Alaska fixed gear ex-vessel market and price transmission from the Tokyo central wholesale market over a time period longer than a

single month (here, six months). In this case, this modeling procedure is somewhat ad hoc in the sense that long-run market integration is not a maintained hypothesis, but nonetheless, the results provide good insight into the nature of short-run market integration.

After experimentation with first-, second-, and third-order polynomials with a six period lag length, we estimated Equation (10) with a second-order polynomial like that given in Equation (12).[7] Direct tests of asymmetric price responses are provided by F-tests on the polynomical lag coefficients (the d's of Equation (12)) corresponding to $(b_j'' - b_j')$ in Equation (10). The parameter estimates of Equation (10) with the second-order polynomial lag are reported in Table 3 and the F-test results are reported in Table 4. A Scheffe interval[8] is used to give a more cautious test by providing a larger critical value than that given by an F-test table due to the experimentation and pretesting used to determine the degree of polynomial.

The significance test results (at a 5% level of significance with a Scheffe interval) indicate symmetric price responses, that is, the response in the Alaska fixed gear ex-vessel market to rising Tokyo wholesale market prices does not differ from responses to declining prices. The results are robust to changes in the order of polynomial from first to second to third and to inclusion or exclusion of an intercept term in Equation (10). Because a first-order polynomial did not give sensible results, the peak Alaska response to a Tokyo price change is not immediate, and does not continuously decline throughout the price transmission period.

The distributed lag estimated under the maintained hypothesis of symmetrical price responses suggests that the peak price response in the Alaska fixed gear ex-vessel market occurs by the end of the third month after a price change in the Tokyo central wholesale market. Moreover, the impact of a Tokyo central wholesale market price change dies out after the fourth month.

TABLE 3.—Parameter estimates of asymmetric price linkages model. Standard errors in parentheses.

Variable	Parameter estimate
c_0	0.05761 (0.18720)
c_1	−0.01289 (0.16581)
c_2	−0.00136 (0.02676)
d_0	−0.00027* (0.00012)
d_1	0.00019 (0.00012)
d_2	−0.00003 (0.00002)

NOTE: Estimates of Equation (10) with second-order polynomial lag structure given in Equation (12). Variable abbreviations are c_i (parameters of polynomial lag for deviations from initial price) and d_i (parameters of polynomial lag for asymmetric price linkages)

* denotes statistically significant at 5%.

TABLE 4.—F-test for asymmetric price responses.

F-statistic	4.23090

F-test for overall significance of d_0, d_1, and d_2 for asymmetric price linkages.

CONCLUDING REMARKS

In this study, we examined the Tokyo central wholesale sablefish market and the Pacific coast and Alaska ex-vessel fixed gear sablefish markets for several forms of long-run and short-run market integration and segmentation over 1981–86.

We found that the Pacific coast fixed gear ex-vessel and Tokyo central wholesale sablefish markets are segmented, so that changes in the Tokyo market prices will have no effect, immediate or lagged, on the prices of the Pacific coast market. The Pacific coast market price instead depends only upon its own lagged values and local market conditions; the ex-vessel fixed gear markets operate independently of the Tokyo central wholesale market over 1981–86. Pacific coast fixed gear harvesters of sablefish are unlikely to be adjusting their sablefish harvesting patterns in response to changes in Tokyo central wholesale market price and demand conditions. While a limited quantity of Pacific coast

[7] A second-order polynomial gave the most sensible shape to the actual distributed lag recovered from the polynomial lag. Moreover, we followed a nested testing procedure for determining the polynomial degree for a given lag length J suggested by Judge et al. (1980). While these results marginally suggested a third-order polynomial, the actual distributed lag (the b's in Equation (10)) recovered from the polynomial lag (given by Equation (12)) indicated a more plausible shape for the second-order polynomial. In any case, the degree of polynomial did not affect the hypothesis test results for asymmetric pricing. Beginning and endpoint constraints were not used, and to be consistent with the Ravallion approach, an intercept term was not included (which would otherwise imply an unexplained constant relationship).

[8] An F-test of linear restrictions using the Scheffe interval adjusts the confidence region, so that the F-test statistic is significant only if it exceeds in magnitude $[(a - 1)F_b]^{1/2}$, where F is the b * 100% critical value for $F(a - 1, T - a)$, T is the number of observations, and a is the number of restrictions. See Snedecor and Cochran (1976, p. 271) for details.

sablefish harvested by fixed gears is exported to Japan so that these markets are integrated by commodity flow on at least a limited scale (but not by price), the low export volume suggests that the Pacific coast producers' export strategy has not aimed at capturing an important market share or establishing a dominant position in the Japanese market. Rather, relatively small-scale U.S. producers are more likely to be simply concentrating on maximizing their net returns in any given time period. Moreover, policy actions and shifting market conditions in one country are unlikely to affect the other.

The Tokyo central wholesale and Alaska fixed gear ex-vessel markets are well integrated by prices in the sense of a long-run tendency in the short-run adjustment process. That is, over a period longer than one month, changes in Alaska prices can be attributed to changes in Tokyo prices and past spatial price differentials between the two markets.

Tokyo and Alaska markets are not fully integrated in the short-run, so that a price change in the Tokyo market is not fully and immediately passed on to the Alaska market within one month. Yet, a form of short-run price integration exists. Alaska market responses to rising Tokyo prices do not differ from responses to declining prices, that is, price responses are symmetric. The peak price response in the Alaska market appears to occur by the end of the third month and the impact of a Tokyo price change appears to die out after the fourth month.

Policy actions or shifting market conditions in Japan will reverberate throughout the Alaska fixed gear ex-vessel sablefish market but not in the Pacific coast fixed gear ex-vessel sablefish market. Should the Alaska fleet continue to orient its harvesting activities toward supplying the Japanese export market, it must contend with the consequent increased vulnerability to any trade, import, and fishing policies implemented by Japan as well as changes in Japanese consumer tastes and preferences. For example, Japanese policy makers might feel that sablefish imports threaten the well-being of Japanese producers domestically culturing or harvesting fish. In this case, because Alaska ex-vessel markets respond to Japanese price changes, a tariff on imported sablefish from Alaska would reduce the price received by the Alaska producers within four months. In turn, changes in Alaska's harvesting patterns would follow sometime thereafter. Alternatively, a Japanese import quota on sablefish would directly restrict the commodity flow from Alaska but not indirectly as with a tariff, which signals through the price mechanism. In contrast, because Pacific coast harvesters do not respond to the information conveyed by Tokyo prices, a Japanese import tariff would be ineffective because it would not impact any commodity flow. Thus, import quotas would be the most effective Japanese policy option to insure that commodity flows are restricted.

U.S. Alaska sablefish policies should be formulated with an eye on the market integration of the fixed gear fleet with the Tokyo market. U.S. policy intentions could be either amplified or dampened, depending upon the situation, creating unintended and perhaps even surprising consequences. For example, U.S. concern over depleting the Alaska's sablefish resource could lead to trip quotas and even contentious gear allocation issues. Yet, if Tokyo prices dramatically rise because of a subsequent restricted Alaska export flow, Alaska harvesters will receive strong market signals to increase sablefish harvests, thereby generating further pressure on the sablefish resource and aggrevating the issues of discards and gear conflicts.[9] Alternatively, if U.S. limitations on sablefish harvests are coupled with say a shift in Japanese consumers' tastes and preferences away from sablefish, leading to a pronounced decline in relative sablefish prices, Alaska producers might respond to these price signals by cutting sablefish production back below the harvest guidelines—thereby obviating the very need of these restrictions. In contrast, if the price linkages present from 1981 to 1986 continue, U.S. Pacific coast sablefish regulations can be formulated without regard to the possible effects upon U.S. production of trends and shifts in the Japanese market or Japanese government policies.

Finally, another form of vulnerability facing U.S. harvesters involves a trade parameter under less direct policy control: changes in the currency exchange rate between Japan and the United States. All prices used in this analysis are converted to U.S. dollars so that fluctuations in the exchange rate will tend to move prices of a traded good in opposite directions within the producing and consuming countries. Price movements observed in the United States and Japan from 1985 to 1987 illustrate the effect of a rapid 40% reduction in the exchange rate. As one indication of increased Japanese purchasing power, real Tokyo wholesale prices for sablefish fell

[9]The price of Pacific coast sablefish are also likely to bid up under this scenario. Through provision of price incentives, the Japanese will encourage methods of harvest, dress, and storage which provide a product suited to their markets (as long as the Japanese hold such a commanding price position in the market).

by 30% during this period. At the same time, real ex-vessel prices for Alaska's longline and pot catch (nearly all of which is exported) rose by 15%, placing them at record highs. Thus the falling exchange rate sent favorable price messages to both U.S. fishers and Japanese consumers, i.e., suppliers were encouraged to provide more fish for export, while Japanese wholesalers were encouraged to buy greater quantities. It is prudent to realize, however, that a reversal in the recent exchange rate decline would tend to produce the opposite effect, sending unfavorable signals to both groups. In such a case, the rising price of the dollar would tend to lower Japanese offers for U.S. sablefish, and, in turn, lower the willingness of American producers to export, if not harvest. The more expensive dollar and reduced supplies would mean higher Japanese domestic sablefish prices, which would reduce their demand for sablefish imports.

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AGGREGATION OF FISH THROUGH VARIABLE DIFFUSIVITY

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ABSTRACT

It is argued that the commonly used model for the dispersal of tagged fish may be inappropriate; for yellowfin tuna at least, it is unable to reproduce the observed spatial variation of abundance. An alternative model, in which the local environment affects both the local population dynamics and the dispersal of fish, is presented.

Fishing is introduced using a simple bioeconomic model; the effect on the distribution of the population is surprising. Routine management questions such as maximizing production become difficult, if not impossible, within this heterogeneous model. Of particular interest are the interactions between a region of high production and its surroundings: at steady state with low rates of exploitation, there is net emigration from areas that can sustain larger populations, but the direction of net migration reverses as fishing pressure increases. Interaction between zones where different technologies are applied is investigated.

Skellam (1951) suggested adopting a diffusion model for the dispersion of inert particles for describing the motility of living organisms, based upon their random motion. Beverton and Holt (1957) put it within a fisheries context, and Jones (1959 and 1976) explained its use in detail. The method is simple: a velocity vector is determined for each recovery, the mean of these is calculated, the differences between each vector and their mean are obtained, and finally the mean of the squares of these residuals is calculated. This term, the "diffusion coefficient" or "diffusivity", a^2, and the mean velocity vector, v, are used to characterize the movements of entire populations. The first governs the dispersion of a population while the second parameterizes any directed, often seasonal, migration.

If there is no directed migration then, for a fish with constant range, the effective area searched per unit time is determined solely by a^2. Analysis of tagging experiments in the eastern Pacific Ocean have not yet shown clear seasonal direction in movements of either yellowfin, *Thunnus albacares*, or skipjack tuna, *Katswonus pelamis*, in this area (Hunter et al. 1986). Directed migration, v, is not explicitly incorporated into the model presented, but could be.

Previous mathematical models for the dispersion of fish have assumed the coefficient of diffusion to be constant, so that the rate of transport due to dispersion is proportional to the gradient of abundance. Bayliff and Rothschild (1974) and Bayliff (1979, 1984), however, reported that estimates of a^2 varied by between one and two orders of magnitude for both yellowfin and skipjack tuna in the eastern Pacific. There appeared to be some pattern to these results; for instance, close to islands and shallow banks, where it has been suggested that prey is more abundant (Sund et al. 1981), a^2 was often less. However, there has been no attempt to formulate the pattern formally, and variations in measured coefficients of diffusion have been treated simply as noise or errors of measurement.

Taking a typical value for the coefficient of diffusion leads to a problem in the case of yellowfin tuna; any single value for a^2 estimated from tagging experiments predicts an almost homogeneous distribution. This is not observed; catch rates tend to be high where prey are believed to be abundant (Sund et al. 1981). Spatial variability of production is unlikely to be sufficient to maintain the variability of abundance that is demonstrated by variability in catch between areas.

This inconsistency does not arise with a variable coefficient of diffusion. Kareiva and Odell (1987) considered a diffusion process for ladybugs preying upon aphids in which the probability of course reversal was increased when the aphid had recently eaten. They showed that this foraging mechanism concentrated predators in areas of high prey density. A similar mechanism is suggested for pelagic fish; if the coefficient of diffusion is a function of local habitat then distributions of tuna can be more realistically simulated. The mechanism involves den-

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sity dependence of the relevant organism, but only indirectly because the density is moderated by the local environment.

For apex predators, such as yellowfin and skipjack tuna, the quality of their environment is determined primarily by the availability of prey; the local degree of saturation by predators is determined by the availability of prey. Saturation is defined as the biomass of predators divided by the maximum that the locality could sustain; thus it is dependent upon the intrinsic richness of the locality and the number competing for those riches. For any particular area, an increase in predators will decrease the availability of prey; this will, in turn, reduce the quality of that area for those predators.

THE MODEL

The biomass of a particular species at any point (x,y) may be modelled:

$$\frac{dA(x,y)}{dt} = F(A(x,y)) + \frac{\partial^2}{\partial x^2}\left(\frac{a^2}{4}A(x,y)\right) + \frac{\partial^2}{\partial y^2}\left(\frac{a^2}{4}A(x,y)\right) - qE(e,y)\,A(x,y). \quad (1)$$

That is to say, the rate of change of the local biomass with time, t, is determined by the production function, $F(A(x,y))$; the catch equation, where q is the catchability coefficient and $E(x,y)$ is the fishing effort expended; plus the diffusion of fish into or out of the locality in both the x and y directions. The key parameter governing diffusion is a^2. It is either constant, or a function of local biomass and carrying capacity; variables that were also in the domain of F.

The production of biomass is modelled using a modification of the Schaefer (1954) model:

$$F(A(x,y)) = A(x,y)\left(r'\left(1 - \frac{A(x,y)}{K'(x,y)}\right) - M\right) \quad (2)$$

where $r' = r + M$ *and* $K'(x,y) = ((r + M)/r)\,K(x,y)$. The modification simply separates natural mortality, M, from the intrinsic growth rate: the modified form uses the gross, rather than net intrinsic growth rate, r. The form of $F(A(x,y))$ is unchanged; the function was rewritten so that birth and death processes would be more explicit. In particular, the carrying capacity is unchanged, as can be checked by multiplying through the above expression for $F(A(x,y))$ by r', and substituting for $K'(x,y)$.

The term a^2 may be a constant, D, or proportional to the local abundance divided by the local carrying capacity. That is to say, unless constant,

$$a^2(x,y) = DA(x,y)/K(x,y).$$

Effort was determined by a simple bioeconomic equation taken from Clark (1985):

$$\frac{dE(x,y)}{dt} = \alpha(pqA - c)\,E(x,y), \quad \text{if } E > 0; \quad (4)$$

$$= 0 \text{ otherwise.}$$

p represents the price per ton received by fishermen, c is the cost to the fishermen of each unit of effort, and α is the proportion of profits reinvested. An implicit assumption is perfect liquidity, i.e., that a loss immediately causes a reduction in effort of the same magnitude as the increase created by a profit.

Equation (1), which represents the kernel of the model, is a nonlinear partial differential equation; it might be possible to solve it analytically, but it is difficult. Solutions were found numerically by iterating explicitly using finite differences.

The 5 million square nautical miles of the range of yellowfin tuna within the eastern Pacific is represented by a grid of 20 × 20 cells, each cell representing an area of approximately 2 degrees in both latitude and longitude. The northern and southern edges of the model grid were joined, as were the western and eastern edges; forming a torus and circumventing any boundary problems. Parameter D was set at 0.08, equivalent to 1,000 square nautical miles per day, a number within the mid range of those found by Bayliff (1984).

The carrying capacity for the region as a whole, and the intrinsic natural rate of increase, were obtained by fitting a Schaefer (1954) model to catch and effort data for this entire region.[2] This gave an annual value for r of 1.61, and an estimate for the carrying capacity of the entire region of 431,000 tons (IATTC in press). The annual rate of natural mortality was estimated at 0.8 by Hennemuth (1961). The catchability coefficient, q, is the probability that a particular fish will be caught by a unit

[2]Patrick Tomlinson, Inter-American Tropical Tuna Commission, c/o Scripps Institution of Oceanography, La Jolla, CA 92037, pers. commun. May 1988.

of effort given that the effort and fish are in the same area, so q has dimension of (1/area). The estimated value of 0.000039 (IATTC in press) for the entire fishery was therefore multiplied by the number of cells, 400, to obtain the q for each cell.

The price of fish, p, was set at \$1,200 per ton, which approximated that of the last half of 1987 (Parks et al. 1988). The cost of a unit of effort, c, was estimated by assuming that in 1987 there existed an economic equilibrium, that is the fishermen just covered their costs in this year but made no net profits. If that were the case, the cost of a unit of effort would be simply the total catch times the price divided by the total effort for that year. This gives c to be approximately \$24,000 per days effort, which was used as the initial value for this parameter when exploitation was included. To evaluate the effect of different restraints upon fishermen in different areas, c was in some cases made position dependent. The proportion of profits reinvested in effort, α, was set arbitrarily at 0.2.

For the initial run all but two cells had carrying capacities set at 1,000 tons; the two exceptions, positioned at (10,5) and (10,10) were given carrying capacities of 10,000 tons. This range of a factor of 10 for the capacities was chosen because it corresponds with the range shown by annual productivity over the region (Berger et al. 1987). The total carrying capacity specified within the model, 418,000 tons, was close to that estimated for the fishery. The abundance for each cell was initially set at the local carrying capacity, except for the cells with the higher capacities where the abundance was 0.8 of that, to speed convergence. Every run of the model was continued until a steady state was evident; the possibility of multiple steady states, implicit in such a nonlinear model was not investigated.

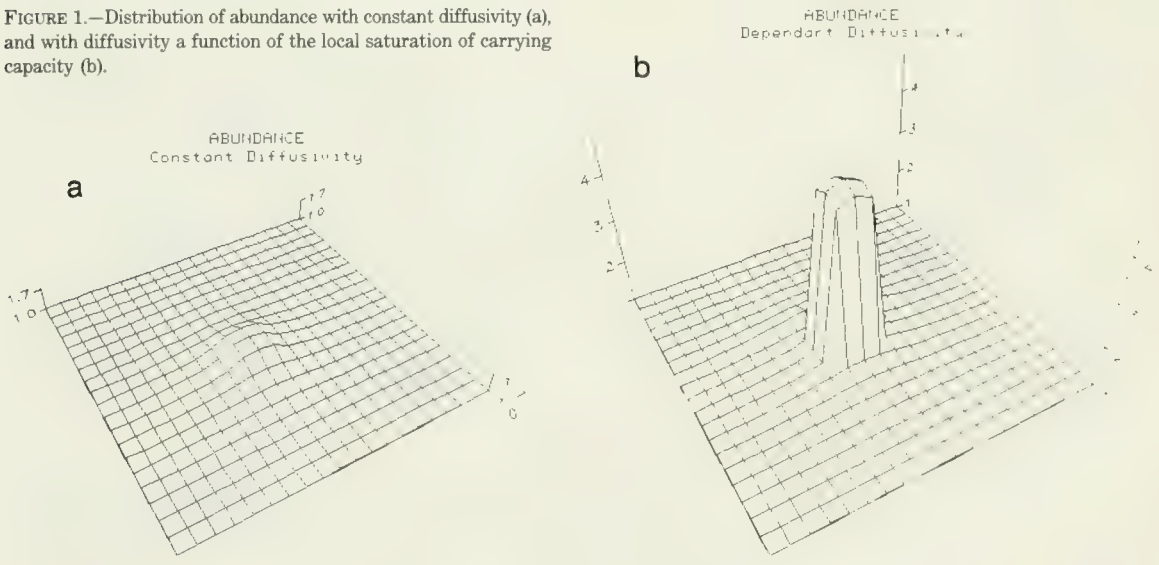
RESULTS

The equilibrium distribution of abundance at zero exploitation was calculated for constant a^2. The abundance of tunas was little higher in the cells of high capacity than elsewhere. This was true even when the "hot" cells were given capacities 100 times that of the others, and when a^2 was reduced by a factor of 10, well below any observed value.

It was believed that if the area of the region of increased capacity were greater, then the leakage of extra production of fish would be less from that region, and a significant local increase in abundance might be seen. By analogy with a coal fire, individual coals cool quickly, but if they are grouped together, they have proportionately less surface area and so cool more slowly. The local increase in abundance was greater when the area of higher capacity was expanded, but most of the increased production of the local area still diffused away. The region of higher capacities was increased to 3×3 cells and even 5×5 cells, but there still was not the sort of variation in abundance that one can infer from catch records. Variations of the same order as appear to occur in the ocean were not found until a^2 was allowed to vary with the degree of saturation of the local carrying capacity.

Figure 1a shows the distribution of fish when

FIGURE 1.—Distribution of abundance with constant diffusivity (a), and with diffusivity a function of the local saturation of carrying capacity (b).



a^2 is constant, and there are 9 cells with carrying capacities 10 times that of the rest. These 9 cells are arranged in a square; the distribution of fish is almost constant. Compare this to Figure 1b, where a^2 is proportional to the degree of saturation of the local capacity. Varying the diffusivity in this way allows the fish to aggregate substantially. This heterogeneity may be maintained even if the cells with higher capacities are not contiguous, as in Figure 2a. The proportion of the biomass in each cell that originated in one of the two anomalous cells is shown in Figure 2b. The data for Figure 2b were prepared by keeping separate account of biomass produced in the two anomalous cells. This

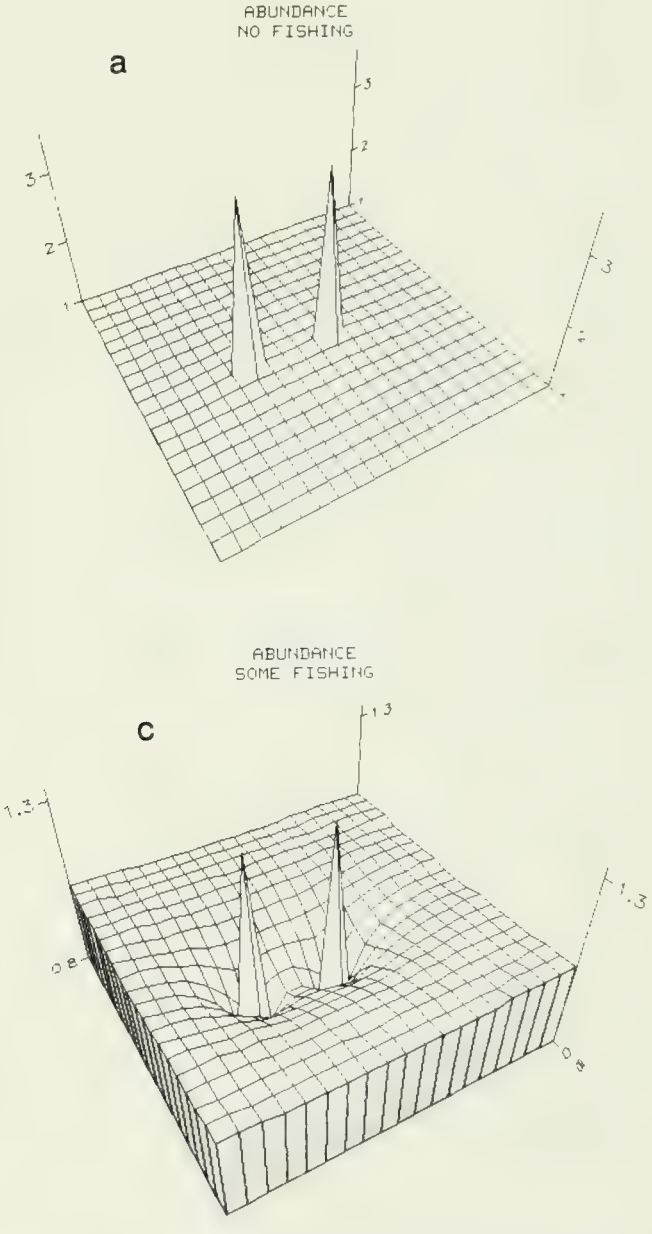


FIGURE 2.—Dependent diffusivity: distribution of fish when there is no fishing (a), and the proportion of the local biomass which originated within the two 'hot spots' (b). Fishing affects both the overall

biomass diffused and died as the rest, in proportion to its abundance; production was determined by the total biomass but ascribed according to location.

Fishing has an effect upon the distribution of fish; the effect is at first surprising (Fig. 2c). A relatively high cost per unit of effort constrains effort; a profit is possible only in those cells with the highest concentrations of fish. In such cells the effort increases until a profit is no longer realized. The abundance has then been reduced to a level that can sustain existing fishing operations, but the catch rate offers no incentive for further investment. From the equation for effort (Equation (4)), the equilibrium

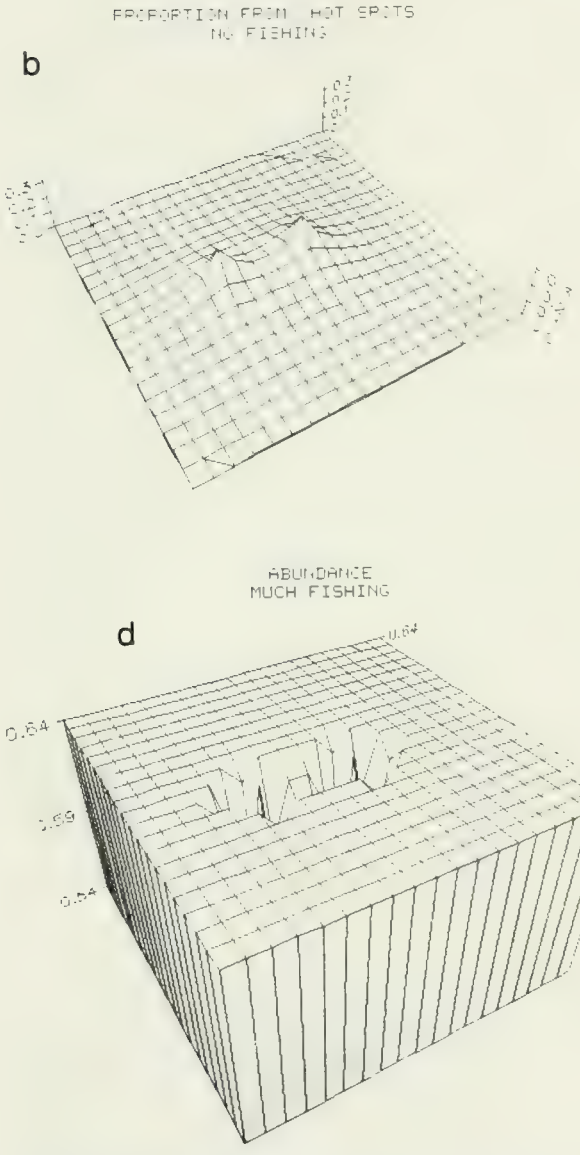


FIGURE 2.—*Continued*—abundance and its distribution (c). Halving the cost of effort halves the level to which the fishery can reduce local populations, and the area of fishing expands to most of the region (d).

abundance of fish in the absence of movement, A^*, would be $A^* = c/pq$. If, say, the cost of fishing, c, is reduced by half, it becomes profitable to increase the effort until the concentration of fish is half of what it was (Fig. 2d). Note also that this reduction in cost allows parts of the region with lower carrying capacities to be exploited. The term A^* determines the maximum equilibrium concentration of fish, and effort increases locally until the abundance of fish is reduced to that level. Effort has a levelling effect upon abundance; it is greatest in the cells with the greatest capacity. In the area immediately surrounding these cells of high capacity, which contain the maximum density, the abundance of fish falls to a minimum because of movement to the cells of high capacity. At this minimum fishing is unprofitable (less than A^*), so there is no exploitation in this area.

It was suggested earlier that regions surrounding islands might consist of enhanced habitat. Cells of higher carrying capacities may contain an island or group of islands with economic conditions significantly different from the rest of the region. The economic parameters need to be different for these cells. This is simply done; the model allows consideration of the effects of economic changes, both local and global, upon the fishery throughout the whole region.

A single island was considered; the island and its waters were assumed to be synonymous with a single cell having a capacity 10 times that of any other cell within the entire 20 × 20 cell region. Three regimes of fishing were considered: low exploitation with the cost of a unit of effort set at $24,000; a regime twice as intensive as a result of halving the cost of effort; and a mixed regime where the single cell of high capacity was exploited according to the parameters of low exploitation, while elsewhere the parameters were as for high exploitation. This could be thought of as a paradigm of development of the fishery if one is careful to ensure that units of effort from different types of fishing are comparable in that they have an equivalent effect upon the target population. It takes many days for a trolling boat to equal the impact a purse seiner has in one day.

The first regime might represent a relatively low level of technological development where further fishing becomes uneconomical while fish are still relatively abundant. Changes in technology might reduce the cost of effort, leading to the second regime with the cost cut by half. The model is such that effort increases everywhere while the abundance of fish is more than half of the previous maximum, and continues to increase until the abundance falls to that level. The mixed regime might represent the case where the higher technology could not be used close to the island because of technical considerations, such as lack of depth for purse seiners, or political ones, such as the prohibition of such fishing to protect artisanal fishermen.

Table 1 shows the effect on catches and sustainable effort of these changes in technology or policy. Technological advancement temporarily increases profits, which leads to greater effort and a decline in catch per unit effort (CPUE). For the parameters used here, the long-term effect of higher technology is to increase the effort expended within the island's waters by 20%, but the CPUE is halved; hence the local catch decreases substantially. Effort is sustainable offshore with the change to the model, and the catch from the newly exploited area is much higher than the total catch which was previously taken only from the island's waters. If the new technology were kept from the island's waters, then the original CPUE could be maintained only by halving the original local effort. Thus, if the new technology were introduced to the high seas, one would expect half as many artisanal boats to be viable, and these boats would catch about half of what had been taken from their waters. If the managers of the island's waters chose to maximize catch by allowing access to the new technology, they could still only stabilize the catch at 60% of what it had been before the advent of the high-seas fleet.

TABLE 1.—Effort and catches at equilibrium under different economic conditions. CPUE at high exploitation is half that at low exploitation.

	Low rate of exploitation	High rate of exploitation	Mixed rates of exploitation
Effort/catch within hot spot	2.03/40.6	2.43/24.3	1.01/20.2
Total effort/catch elsewhere	0.0/0.0	38.53/385.3	39.29/392.9

DISCUSSION

Although I feel certain that constant diffusivity is an inappropriate model for tunas, there may other models at least as appropriate as that presented here. (See Okubo (1980) for an extensive review of diffusion within models of ecology.) If the basic structure of the model were correct; the assumption that a^2 is a linear function of local saturation might not be. The structure of the model is testable;

in particular it predicts that heavy fishing will enhance immigration. In a practical model, one might use a^2's directly when possible and find a convenient empirical function for indirect estimation of a^2 at other times.

The dimensions of a^2 are (distance^2/time); a^2 can be thought of as the average distance moved before taking another direction, multiplied by the mean speed over that interval (Beverton and Holt 1957). Even at constant speed, an individual fish can reduce its a^2 simply by changing course more frequently, so the fish could maintain an almost constant position if it were to change direction frequently enough. The upper limit is determined by the fish's ability to hold a course. Walker et al. (1985) showed that yellowfin tuna can detect a geomagnetic field and suggested that they might use it for navigation. This appeared incongruous in a fish whose direction at any time is said to be random. But, if it allows each fish to hold any random course longer, then it allows the fish to get away from an area it has found to be unsatisfactory. Fish in an isolated undesirable area will all be, in a sense, navigating away from that area, but in different directions; that is why the population in that area does not exhibit any directed migrations; they all cancel each other.

Given that there is heterogeneity in the distribution of prey, it is not surprising that predators have evolved towards matching that distribution. A fish cannot know where the greatest concentrations of prey are and then navigate to them, but it can reduce the chances of leaving a favorable region and increase its search area when hunting is poor. A tuna varying a^2 inversely with habitat quality has advantage over any with constant a^2. In poor habitat the fish has high a^2, and its net movement over any period is greater. Upon entering a more favorable area, a^2 drops, and the fish weaves a more intertwined track over a smaller area. Thus the individual spends more time in the more favorable areas; a population of such individuals accumulates in the better habitat without any directed migration.

The most patently unrealistic aspect of this model is its topology, that of a torus. This is a convenience chosen to avoid boundary conditions at the spatial limits of the model and to avoid speculating about an additional mechanism that maintains the fish within those limits. Specifying more realistic boundary conditions might include seasonal changes in the positions of those boundaries.

A species constrained within such plastic boundaries would demonstrate seasonal changes in distribution, and tagging would suggest directed movement. But, no long-range directed navigation would be necessary. At one end of their distribution, as the boundary of intolerable conditions encroaches, fish might retreat, or simply die. Elsewhere the population might simultaneously be expanding by the chance movement of individuals into freshly habitable waters.

For those species whose directed movements are real, one can simply add a term, v, to the model. Determining the (time varying) values for this might require more tagging effort than that required simply for evaluating a^2.

There is probably some autocorrelation in the direction of movement of the fish, but this would not affect the conclusions drawn from this model. Individuals emanating from a point source at first show a clear orientation away from this source; if each individual's course exhibits autocorrelation, then this orientation persists but diminishes through time. Eventually the individuals lose their orientation to the source, and direction is independent of position. The void initially created at the source is filled, and the simpler diffusion equation may be considered an acceptable model for describing the distribution of individuals (Skellam 1973).

In a more realistic model, the topography of the environment would be very complicated, with variation at many scales. This model is a very inexact description of the population it purports to describe (yellowfin tuna in the eastern Pacific), but habitat dependent diffusion may be applicable to other regions and other species. Kleiber[3] has shown that the simple diffusion model is also inadequate for skipjack tuna in the western Pacific. Beamish and McFarlane (1988) suggested that the dispersal of adult sablefish may be affected by the local density. Sablefish are much more sedentary than tunas; Beamish and McFarlane estimated that local fluctuations of abundance are determined by recruitment of juveniles and by fishing.

Scientists who have examined data for tunas tagged close to islands refer to two populations: one which remains associated with the islands, which must have a low a^2; and one that breaks away, which necessarily has a higher value for a^2. Individuals that leave one island are, of course, still susceptible to "capture" by another island, or perhaps a shallow bank. The model described here suggests

[3]Pierre M. Kleiber, Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. June 1988.

that the difference in a^2's is more an effect than a cause of their positions.

Figure 2b makes an important point. Although, in the absence of fishing, the anomalous cells (the "hot spots") act as a net source of fish to the entire region of the model, there is still much mixing of fish into these sources. The importance of mixing depends upon the rate of dispersal of fish, mortality rate, and the distance involved. In this case, it is clear that it would be foolhardy, having divided the region into "substock areas", to then try to manage these areas in isolation.

The effect, seen in Figures 2c and 2d, that fishing has of creating a minimum in the abundance close to the maximum, needs to be explained further. Figure 2a shows the steady-state abundance before any extraction of fish; the net flux through each cell is zero. The probability that a given individual within each cell migrates must be inversely proportional to the number of others within that cell, as otherwise the total emigrating would not be constant for all cells. Let us suppose that fishing starts in just one cell, that with most fish. The balance of migration is temporarily disturbed. Fish move in at the same rate as before but, because there are now fewer fish inside than there were, there is less emigration from that cell. This causes a net flow towards the cell that is being fished despite the fact that this cell still contains more fish; the variability of a^2 allows flow "uphill", against the gradient in abundance. The flow to the cell being fished causes the abundance to drop in its neighbors, which then stimulate a net flow from cells more distant from the fishing. A dynamic equilibrium is established when the amount removed by fishing is met by a balance of local production and net immigration to the cell of exploitation. This immigration is fed by the rest of the region, where carrying capacity is constant and flow is "downhill". The transport of fish towards exploitation is maintained by a gradient of abundance and amplified by the differences in a^2 created by that gradient. Fishing at the places of highest capacity makes them sinks for the entire region, drawing fish in from everywhere. The ability of a fishery to mold the topography of the abundance may lead to a founder effect in (model) fisheries. An established fishery will depress the abundance in the surrounding region, which may make fishing uneconomical. This might not have been so if fishing had started simultaneously.

There is no clear evidence, as far as I am aware, that abundance minima surround areas of exploitation. It is the bane of fisheries science that little information is obtainable from marginal areas; most of our information comes from fishermen who do not generally choose to work where they expect fewer fish. In a more realistic model, with habitats changing realistically (time-scales of a few hours), the system may rarely be near equilibrium. This, and the fact that there is variability on very different scales in space as well as time, make it unlikely that the simple topography illustrated here would be seen in practice. Indeed, most fishermen would suggest that the spatial and temporal topography of abundance is extremely complicated. The variability of q, the notional catchability coefficient, may be due to changes in the degree of aggregation of the fish. Too disperse and the fish may not be economic to catch. Too aggregated and a few boats might be fortunate, but they would be overwhelmed and unable to fully exploit what they had found.

Migration of fish between different fishing areas tends to diminish the attraction of catch reduction as a management tool to a manager responsible for just one of those areas; high rates of exploitation effectively enlarge the range of the fishery. With a^2 a function of the immediate environment, the effect is enhanced; reducing the catch reduces immigration and enhances emigration.

Within the Schaefer (1954) model, biological production is highest at half the carrying capacity. Figure 2a shows that the abundance at the hot spots, while higher than elsewhere, is less than 40% of the carrying capacity of those spots. In this sense the populations of fish at the "hot spots" are below optimum, even before any fishing takes place. Fish are exported to the surrounding region, increasing the abundance there to more than the local carrying capacity. Thus the surrounding region has negative net production. Maximizing local production everywhere is impossible, and working out the distribution of effort that would lead to maximum overall production would be difficult. Harvesting outside of the hot spots would reduce the abundance of fish at these hot spots and so reduce the productivity there still further. Regardless, it is unrealistic to suppose that a total ban on fishing where catch rates are highest is feasible, or even desirable. The economic portion of this model allows us to investigate the effects of intrinsic change and less intrusive management.

Table 1 indicates that the effects of an increase in power of the fishery may not be positive in a region where the fishery is viable before the change. Here power denotes the technology that allows fishing to be viable at a particular index of abundance of fish. Reducing the cost, as was done ex-

plicitly within the model, has the same effect as increasing catchability or, perhaps through improved handling and distribution of the fish, raising the price. Whatever the reason, increasing power allows fish to be profitably caught when there are fewer of them. This enables fishing to take place at locations other than the hot spot, but the change reduces the catch at the hot spot even though effort there increases. There is the familiar reason of local overexploitation, but also the reduction in fish elsewhere decreases the flow of fish to the hot spot. If the hot spot contains an island with a government that can create local restrictions on effort, the local catch rate could be held at the original level only by drastically reducing the effort to far less than that of the original local fishery. This might prove a difficult choice for a small island dependent upon fishing.

CONCLUSION

A constant value for a^2 creates an unrealistic, almost homogeneous distribution of fish. A variable a^2 allows fish to spend more time in good habitats. They can vary a^2 by changing direction more or less frequently. Preliminary observations indicate that a^2 does vary as this notion predicts.

Fishing, by removal of competing individuals, increases the potential production of a surviving individual; thus the habitat appears enhanced and migrants are more likely to stay. In this way fishing has an impact far beyond its location. The catch rate close to an island is partially sustained by tapping the resources from the contiguous region. An effect of a high-seas fleet is to reduce the gradient of habitat saturation from what would occur if there were only fishing close to islands; thus the relationship between a high-seas fleet and artisanal inshore fishery is clearly competitive.

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MASS MORTALITY OF SCIAENID FISHES IN THE GULF OF NICOYA, COSTA RICA[1]

An unusual fish mortality, nearly specific for the family Sciaenidae (corbinas, croakers, drums), is reported for the Gulf of Nicoya, Costa Rica. The gulf is a large, estuarine embayment located on the Pacific coast of Costa Rica (Fig. 1). Its waters provide roughly 50% of Costa Rican commercial finfish landings, with sciaenids accounting for about 43% of the artisanal catch, or about 2,700 metric tons per year (Araya 1984; Ministerio de Agricultura y Ganadería unpubl. data 1985).

Initial observations of the mortality by residents of the inner gulf were made in late September 1985. By mid-October, extensive sciaenid mortalities had been reported throughout the inner gulf northwest of Puntarenas and Playa Naranjo, and observed by us in the middle of the gulf between Puntarenas and Isla Chira (Fig. 1). Local fishermen noted that fishes were not affected in the gulf oceanward of Puntarenas. They also noted that members of the corbina

[1]CIMAR Contribution No. 138.

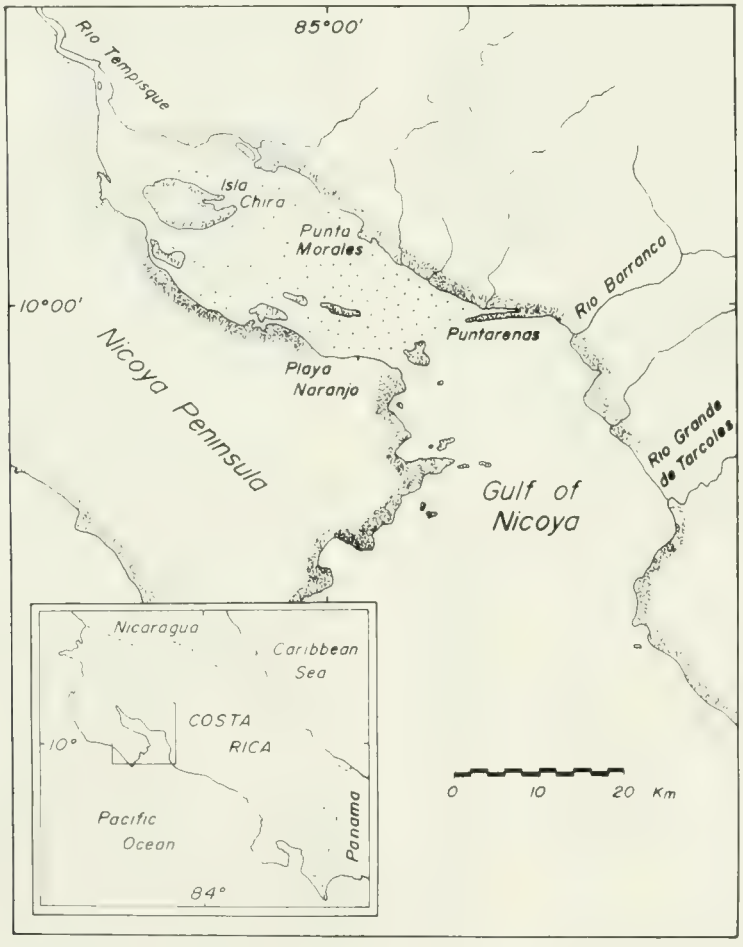

FIGURE 1.—Gulf of Nicoya, Costa Rica. Shading indicates suspected extent of sciaenid mortality.

family were almost exclusively killed, particularly the commercially important *Cynoscion squamipinnis*. Mortalities appeared to decline by late October, and after 4 November, no sciaenid mortalities were reported.

Six fish collections were made between 12 October and 4 November 1985 in the vicinity of Punta Morales, by following flotsam windrows in a skiff and indiscriminately collecting fishes from the water surface with a landing net. Collections lasted from 1 to 2 hours, and the fishes were subsequently sent to the laboratory and identified.

Fishes taken in the collections were almost entirely (98%) sciaenids, including 15 sciaenid species from 7 genera (Table 1). Affected sciaenids ranged in size from 46 to 490 mm SL. Species observed in the mortality, but not taken in the quantitative collections, included *Anchovia macrolepidota*, *Oligoplites* sp., *Chaetodipterus zonatus*, *Sphoeroides tricocephalus*, and the sciaenid *Cynoscion stolzmanni*.

Nearly all fishes were dead upon collection, with few moribund individuals observed. Dead fishes were generally found floating belly-up, while the moribund ones often were floating motionless and taking slow, intermittent breaths. No lacerations or other obvious external marks were noticeable at the time of collection, and most of the fishes appeared fresh. Digestive tracts of several examined specimens were empty. Some of the larger species were collected by local fishermen and eaten or sold for food, with no apparent deleterious effects.

TABLE 1.—Fish species taken in periodic collections during fish mortality in the Gulf of Nicoya, 12 October–4 November 1985. Data pooled for six collections.

Species	No. collected	Size range (mm SL)
Sciaenidae		
Bairdiella armata	1	114
Cynoscion phoxocephalus	45	54–300
C. squamipinnis	162	46–490
Isopisthus remifer	6	180–200
Micropogonias altipinnis	1	151
Ophioscion sciera	6	111–217
O. typicus	4	113–139
Ophioscion sp.	11	91–149
Paralonchurus dumerilii	4	162–314
Stellifer chrysoleuca	2	154–230
S. furthii	36	105–164
S. illecebrosus	18	85–229
S. oscitans	112	66–148
S. zestocarus	7	89–115
Stellifer sp (undescribed)	7	82–105
	422	46–490
Other families		
Muraenesox coniceps	1	640
Ilisha furthii	2	220–243
Ariopsis seemani	1	194
Pomadasys macracanthus	1	335
Trichiurus nitens	3	397–800
	8	194–800

Four moribund sciaenids (3 *Cynoscion squamipinnis*, 1 *Ophioscion sciera*) and a puffer (*Sphoeroides tricocephalus*) were collected and preserved in 10% buffered formalin (pH 7.2), and the internal organs were sectioned and stained using standard histological methods. Control sections were made from *C. squamipinnis* and *C. phoxocephalus* collected several months after the mortality. Major macroscopic abnormalities in all specimens included

1) Presence of petequial hemorrhages in the oral cavity, gill arches, operculum, and base of the pectoral fins.
2) Destruction of the distal third and hyperemia in the proximal two-thirds of the secondary gill lamellae.
3) Presence of blood and blood clots between the two layers of the pericardium.
4) Pronounced paleness of the liver, very crumbly upon cutting.
5) Congestion and hemorrhages in the intestinal serosa. Fibrous bands adhering some segments of the intestinal serosa to the abdominal wall.
6) Kidney and spleen crumbly and of a semiliquid consistency.
7) Gastrointestinal system containing a yellow-green mucous.

Major microscopic findings included

1) Large numbers of eosinophilic granulocytic cells in the submucosa of the gastrointestinal system, apparently in response to a high load of nematode and intermediate stage cestode parasites encysted in the layers of those organs. Intense development of connective tissue around the peripheries of those parasites.
2) Necrosis of haemopoietic tissue of the spleen with the proliferation of melanomacrophage centers.
3) Generalized vacuolar degeneration of the hepatic parenchyma with areas of extensive necrosis.
4) Necrosis of renal hematopoietic tissue and degeneration of the renal tubule epithelium (nephrosis).

The combination of tissue irregularities observed is compatible with pollutant-induced damage (King 1962; Buhler et al. 1969; Walsh and Ribelin 1975), but we have no direct evidence linking pollution to the mortality. We suspect that an agricultural toxin may be involved because a large number of agrochemicals are currently in rather indiscriminate

use in the area. The beginning of the year's heavy rains in late September could have served as a vector for an agrochemical. Also, a fish mortality of unknown cause in Lake Arenal, located approximately 45 km NE of the upper Gulf and draining adjacent lands, occurred simultaneously with the sciaenid mortality, killing primarily *Cichlasoma nicaraguense* (J. Cabrera[2]). However, in neither case were there reports of dead fishes or invertebrates in nearby rivers that might serve to transport an agrochemical. Tests detecting the presence of possible pollutants were not available. The possibility that the sciaenid deaths were caused by toxins from red tides that occurred in parts of the gulf between April and November (Víquez 1985; R. Víquez[3]) cannot be ruled out. Likewise, disease cannot be discounted, although attempts to isolate any infectious agents (bacteria, fungi) from fresh specimens were unsuccessful.

The near specificity for sciaenids remains a mystery, and we are not aware of any other fish kill specific at the family level. Cardeilhac et al. (1981) reported acute deaths of large red drum (a sciaenid) in Florida, which they attributed to metal poisoning resulting from ingestion of contaminated prey. Gulf of Nicoya sciaenids are generally bottom fishes known to consume a variety of benthic fishes and invertebrates (Araya 1984). Their benthic distributions or food habits alone do not explain their susceptibility because a large number of benthic fishes with similar food habits are common in the gulf (León 1973). The wide size range of sciaenids affected also argues against the specificity being due to consumption of common prey.

No measure of total number of fishes killed in this mortality is available. However, we estimated that at its height (mid-October), a thousand fishes could be sighted along a few hundred meter stretch of a flotsam windrow. Since the mortality, fishermen reported no noticable decline in the catch of sciaenid species. Although no mortalities of this nature have been reported in the past, their recurrence could endanger the livelihood of Gulf of Nicoya fisheries.

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[3]R. Víquez, Universidad Nacional, Heredia, Costa Rica, pers. commun. October 1986.

GROWTH AND SURVIVAL OF EARLY JUVENILE AMERICAN LOBSTERS, *HOMARUS AMERICANUS*, ON A DIET OF PLANKTON

Larval American lobsters, *Homarus americanus*, are planktonic and are known to feed raptorially on zooplankton (Herrick 1895; Williams 1907; Templeman 1936). However, the benthic, postlarval stages of the American lobster are not routinely found in the field, and their natural habitat and feeding behavior are not known. Consequently, the natural diet of these stages is unknown. Stomach content analyses of larger juveniles and adult lobsters show that they feed on a great variety of benthic animals, including polychaetes, molluscs, macroalgae, and other crustaceans (Leavitt et al. 1979; Carter and Steele 1982).

Older juvenile and adult American lobsters, however, seem to have fundamental differences in their behavior compared with the early juvenile stages used in this study. Laboratory studies and field observations indicate that early juveniles are more (perhaps exclusively) shelter bound (as Cooper unpublished data in Cooper and Uzmann 1980; Lawton 1987; Barshaw and Bryant-Rich 1988). If the early juveniles do not forage for food outside of their burrows, they must feed in a different manner and on a different diet than that of older lobsters. During behavioral observations in naturalistic substrates, early juvenile lobsters were seen to generate a current through their U-shaped burrows by pleopod fanning (Barshaw and Bryant-Rich 1988). They appeared to catch and feed on the plankton that was carried in by this current. These observations form the basis for the hypothesis that early juvenile lobsters can feed upon plankton.

Materials and Methods

Stage IV lobster siblings from the Department of Fisheries and Oceans Laboratory, St. Andrews, New Brunswick, Canada were held in plankton "kreisels" (Hughes et al. 1972) for one day after being transported to Woods Hole, MA. These lobsters had all molted into Stage IV approximately two days before they were transported and were all fed on frozen brine shrimp until the experiment started. At the start of the experiment, individual lobsters were placed into 72 trays (22 cm long × 6.4 cm wide × 5 cm deep; water volume = 750 mL). Each tray was provided with filtered, ambient, running seawater, kept on a natural light/dark regime, and had an artificial lobster shelter made of black tubing glued to the bottom. The lobsters were allowed four days to acclimate to the trays before the experiment began. During this time, all of the lobsters were fed once on frozen brine shrimp (*Artemia*), and any dead lobster was replaced by another sibling. The 72 lobsters were then randomly divided into three groups of 24; one group was starved, one group was fed daily on five frozen brine shrimp per lobster, and the last group was fed daily on plankton. Dead, settled plankton was not used; only plankton which appeared living was presented to the lobsters. The trays were cleaned daily and any uneaten shrimp or plankton were removed.

The plankton was collected every other day by plankton tows in the Woods Hole area. After collection, the plankton was sieved through a 1 mm mesh. Half of the plankton was kept alive for 24 hours, while the rest was fed to the lobsters immediately. Representative subsamples from the daily portions were rinsed with distilled water, filtered, dried, and weighed; the same was done with the daily portion of frozen brine shrimp.

For one hour at the onset of feeding, the flow of seawater through all the trays was stopped so that the plankton-fed lobsters had a chance to feed before the plankton was flushed out of the trays. During this hour, informal observations were made on the behavior of the feeding lobsters. Movements of the lobsters in the trays, pleopod-fanning and mouth part activity were observed.

The experiment continued until all surviving lobsters had completed two molts; this took 65 days, from 14 October to 17 December 1984. During that time, all molts and deaths were recorded. The lobsters' weight and carapace length (CL) were taken after 40 days and at the end of the experiment. To make these measurements, each lobster was carefully removed from its tray and placed on absorbent paper to remove excess water. The lobster was then weighed to 0.01 mg on a Mettler balance; CL was measured to the nearest 0.1 mm using calipers. This procedure took less than two minutes and did not appear to adversely affect the lobsters.

Results

There was no significant difference in American lobster survival between the group fed brine shrimp (75% survival) and the group fed plankton (83% survival). All of the starved lobsters died by day 39 of the experiment (Fig. 1). This group is significantly different from the other two (χ^2, $P < 0.001$).

Nine of the starved lobsters molted to Stage V before dying. All of the surviving lobsters in the two

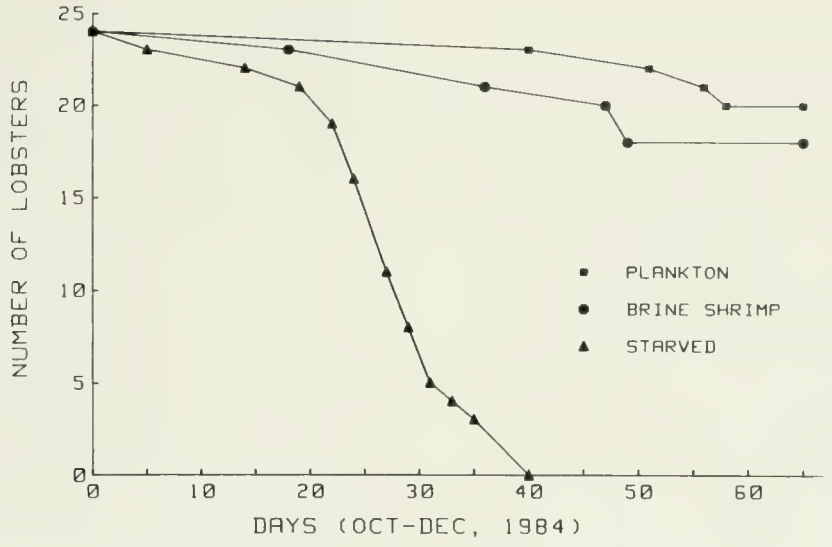

FIGURE 1.—The number of lobsters surviving in each treatment over the time course of the experiment.

fed groups molted twice during the experiment ending at Stage VI. There was no significant difference between the two fed groups in the number of days from Stage IV to Stage V. However, the plankton-fed group took an average of 34 days to molt from Stage V to Stage VI, significantly longer than the brine shrimp-fed group which took 23 days (Students t-test, $P < 0.001$; Fig. 2).

Both fed groups showed significant increase in CL and weight (Students t-test, $P < 0.001$). The group fed brine shrimp grew more; they were significantly larger (Students t-test, $P < 0.05$)

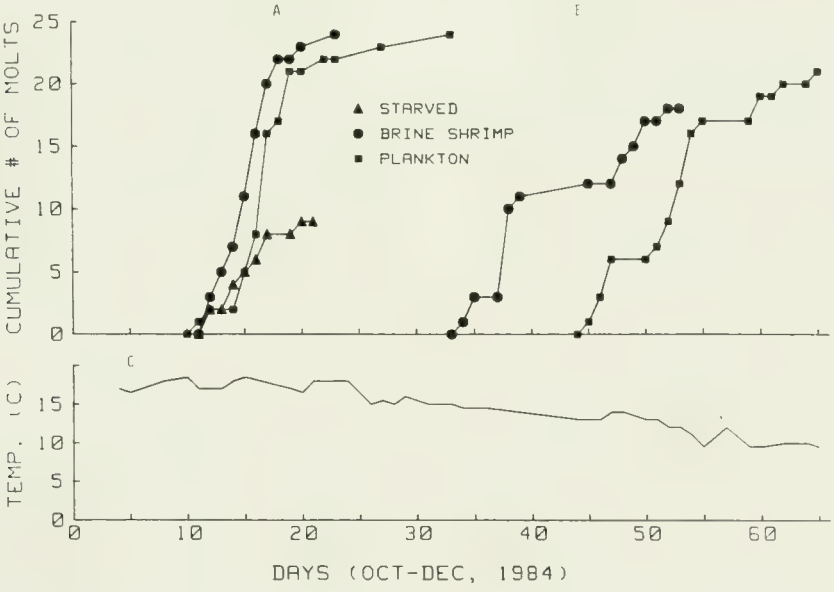

FIGURE 2.—The cumulative number of lobsters in each treatment molting from (A) Stage IV to Stage V and (B) Stage V to Stage VI.

and heavier (Students t-test, $P < 0.001$) at the end of the experiment than the group fed plankton (Fig. 3).

The brine shrimp-fed lobsters were observed to routinely leave their burrow in order to obtain the brine shrimp which was fed to them daily. They would then return and eat inside of their shelters. The plankton-fed lobsters behaved differently. After the plankton was placed in their tray, they would begin vigorous pleopod-fanning while remaining in their shelters. Plankton was seen being drawn into their shelters by this fanning.

The average dry weight of the plankton fed to the lobsters daily was 2.6 ± 1.4 mg, while the average dry weight of the brine shrimp fed to the lobsters daily was 5.0 ± 4.7 mg. The water temperature ranged from 18.5° to 10°C, averaging at 14.7°C.

Discussion

Emmel (1908) found that Stage IV lobsters could molt to Stage V without being fed when they were kept in flowing unfiltered water. Daniel et al. (1985) showed that early juveniles can survive and grow on a diet of frozen barnacle larvae. Budd et al. (1978) showed that the young crayfish, *Orconectes immunis*, can filter feed on algae by creating a feeding current and catching the algae in a filter formed by the first maxillipeds and their maxillae. Factor (1978) suggested that the mouthparts of larval lobsters have enough setae placed appropriately to make filter feeding a possibility. Upon close examination of Factors's data on Stage IV lobsters, it is seen that this stage has even more setae than the three previous stages. Recently, Kari Lavalli[1] has extended Factor's study, finding that lobsters, at least up to Stage VI, continue to have appropriately placed setae for catching plankton. Thus, morphologically, postlarval lobsters seem to be capable of catching plankton.

This experiment has shown that while the unfed postlarval lobsters all died, lobsters fed plankton survived as well as lobsters fed brine shrimp. The lobsters fed plankton also showed a significant increase in carapace length and weight. Therefore, these lobsters were able to catch and consume live plankton resulting in a net energy gain. Templeman (1936) found that lobsters held at 13°C took 29 to 30 days between their fifth and sixth molt; therefore, the rate of molting in the brine shrimp-fed group fell well within the rate of normal, nonfood limited molting at a temperature of 15°C.

[1]Kari Lavalli, Boston University Marine Program, Marine Biological Laboratory, Woods Hole, MA 02543, pers. commun. 1988.

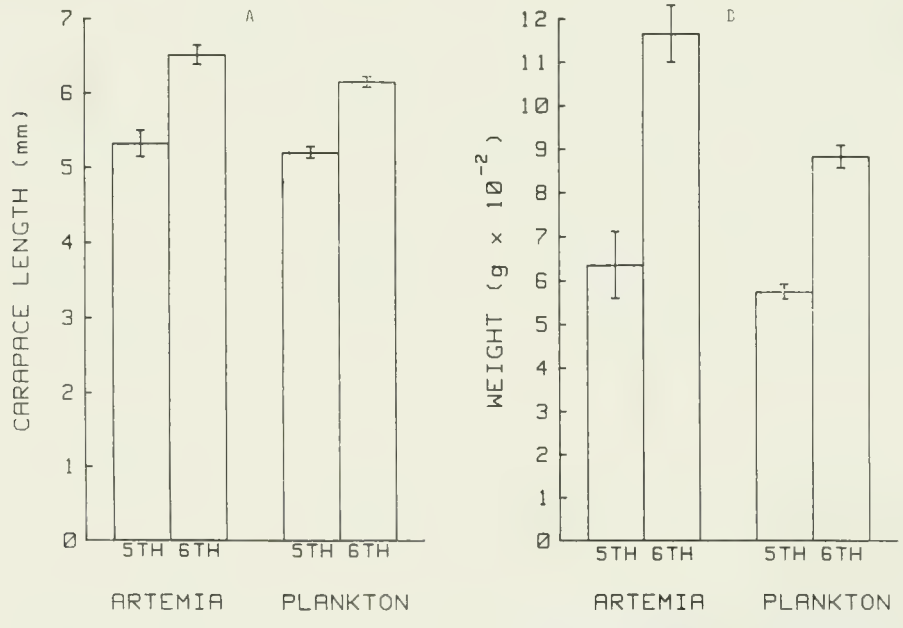

FIGURE 3.—The (A) carapace length and (B) weight of the *Artemia* (brine shrimp) fed lobsters and plankton-fed lobsters at Stage V and Stage VI, (C) water temperature over the time course of the experiment.

The amount of plankton that was given to the lobsters fell within the upper range of natural plankton densities found in Narragansett Bay, RI (Durbin and Durbin 1981). Juveniles living in deeper water would, of course, be unable to feed on algae and upper water plankton. However, suprabenthic plankton and swarming epiplankton are also plentiful (Cornet et al. 1983; Sainte-Marie and Brunel 1985) and could be caught in the same manner as the upper water plankton. I fed the lobsters in this experiment upper water plankton because evidence to date shows early juveniles to settle in shallow subtidal areas (as Cooper unpublished data in Cooper and Uzmann 1980; MacKay 1926; Hudon et al. 1986; Able et al. 1988). I do not wish to suggest that early juveniles feed exclusively on plankton; they also eat small benthic organisms in the vicinity of their burrows (Berrill 1974; Barshaw and Bryant-Rich 1988).

In this experiment, lobsters in the brine shrimp treatment were seen to routinely leave their shelters. While in a long-term experiment, lobsters never were seen out of their burrows (Barshaw and Bryant-Rich 1988). Perhaps these observations indicate that early juvenile lobsters more readily leave an artificial shelter than a burrow they construct themselves in a relatively natural habitat. Also, in this experiment, if the lobsters in the brine shrimp treatment had not left their shelters, they would have been unable to eat.

Many investigators have suggested that early juvenile lobsters do not leave their burrows in nature (e.g., Cooper unpublished data in Cooper and Uzmann, 1980; Atema et al. 1982; Barshaw and Bryant-Rich 1988), but this idea poses the problem of how the lobsters then forage for food. The results from this experiment indicate a mechanism by which settled lobsters can fulfill all of their energy and nutritional requirements while remaining in their burrows.

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BEHAVIORAL OBSERVATIONS ON FIN WHALE, *BALAENOPTERA PHYSALUS*, IN THE PRESENCE OF KILLER WHALE, *ORCINUS ORCA*

Detailed observations of baleen whales attacked by killer whales, *Orcinus orca*, are scarce. Most of these records involve attacks on gray whales, *Eschrichtius robustus* (e.g., Scammon 1874; Gilmore 1961; Morejohn 1968; Pike and MacAskie 1969; Rice and Wolman 1971; Baldridge 1972). Although reports exist of killer whale tooth marks on different body parts of fin whales, *Balaenoptera physalus*, sei whales, *B. borealis* (Hoyt 1981), minke whales, *B. acutorostrata* (Jonsgård 1968), and bowhead whales, *Balaena mysticetus* (Tomilin 1967); and although remains of some of these species (fin, sei, and minke whales) have been found in stomachs of killer whales (Nishiwaki and Handa 1958; Tomilin 1967; Rice 1968; Hoyt 1981; International Whaling Commission 1982), we know of only a few reports of direct observations of killer whales attacking mysticetes besides gray whales. These include attacks on 1) southern right whales, *Eubalaena australis* [= *glacialis*] (Cummings et al. 1972); 2) a humpback whale, *Megaptera novaeangliae* (Martinez and Klinghammer 1970); 3) a minke whale (Hancock 1965); 4) a female sei whale with a calf (Gaskin 1982); 5) a fin whale (Pike and MacAskie 1969); and 6) an immature blue whale, *Balaenoptera musculus* (Tarpy 1979). Of these authors, only Hancock (1965) and Cummings et al. (1972) provided some detailed behavioral observations.

In this paper, we describe the behavior of a group of fin whales in the presence of three killer whales and discuss these observations with regard to the available literature.

Field Observations

While searching for gray whales on 2 March 1982 (0850 h), we headed offshore from Tojahui (lat. 26°37′N, long. 109°23′W), a small fishing camp approximately 9 km SE of Yavaros, Sonora, in the Gulf of California, México, in a 5 m dory powered by a 75 hp outboard motor. Sea conditions were excellent with a calm and glassy water surface, no wind, and visibility about 6 km. Twelve km from shore, over a water depth of 50 m, we encountered a large group of 20 fin whales, judged to be adults (estimated total lengths ca. 18–20 m). We stopped the boat and motor within 40–300 m of the whales, and began observing their behavior. The whales formed closely spaced pairs or triplets within <5 m of each other and were lunge-feeding at the surface on dense patches of fish larvae and other macroplankton. The whales continued in this activity for 20 minutes, while forming a large semicircle off the stern of the boat at distances ranging from ca. 50 to 500 m (Fig. 1). None of the whales appeared to be moving in any definite direction.

While we were photographing a pair of fin whales swimming slowly north, 50 m from the boat and parallel to it, we sighted several killer whales ca. 200 m from us and heading in the direction of the pair. The killer whales were moving extremely fast and disturbing the water surface. The pair of fin whales continued swimming in their original direction for 30 m and then abruptly changed direction, by about 65°, increased their speed notably, and moved towards the boat (Fig. 1). At that time the killer whales were 60 m behind the fin whales, and the two sets of whales and the boat were all in straight line. As the killer whales moved to 20 m from the boat, the fin whales disappeared just below the surface, and at that instant, a killer whale's head protruded above the water with its mouth open and teeth visible. There were two other killer whales slightly behind the first one. Judging by the size and shape of their dorsal fins, all three individuals were females or immature males. The pair of fin whales

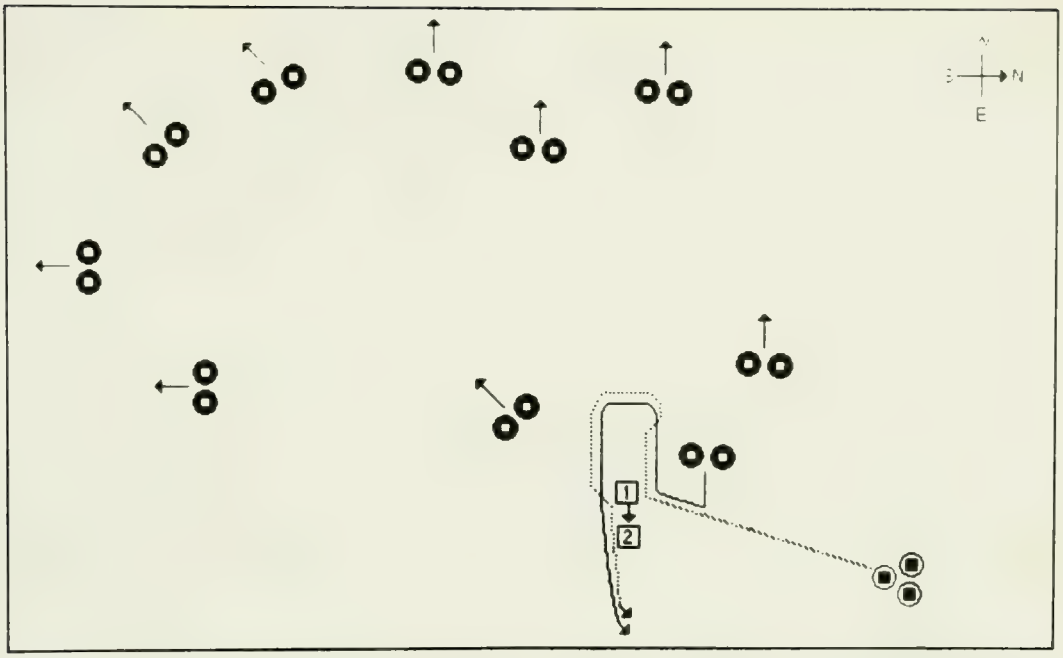

FIGURE 1.—Schematic representation (not to scale) illustrating the sequence of the killer whale–fin whale interaction. Dark squares in light circles = the three killer whales; light squares in dark circles = fin whales; the two numbers inside squares = the boat with observers at initial and final positions; solid and dashed lines with arrows = movements of the principal fin whale pair and the three killer whales, respectively.

and the killer whales were still headed directly towards the boat at an estimated speed of 30–40 km/h. Aware of the risk of staying in the path of these whales, we started the motor and moved 30 m east. Just after starting the motor, the pair of fin whales changed direction by about 110° and headed towards open sea (Fig. 1), probably as a result of our movement. The fin and killer whales continued west for 50 m and were now approximately 80 m ahead of us. During this encounter, we heard at least six clear, high pitched whistling sounds that each lasted about three seconds.

We then observed one of the killer whales turn towards the pair of fin whales. At this moment, the fin whales turned approximately 180° and headed back towards the boat, in the direction of land. The pair, with the three killer whales close but slightly behind them, continued towards the boat. When they were 5 m away and parallel to the boat, we saw the head of one of the fin whales disappearing below the water. At that same moment, the head of one killer whale appeared above the fin whale. At this time we observed a great amount of splashing created by both species. The pair of fin whales then continued swimming east, with many short surface dives each lasting between 5 and 10 seconds. The killer whales continued their pursuit. All whales were travelling too fast for us to follow them, and they were soon out of sight.

During the time of the killer whale–fin whale interaction, the other fin whales that were not directly involved were all swimming very slowly out towards open sea, showing almost no parts of their bodies and with no visible or audible blows, possibly to avoid detection. We followed them and finally counted at least 13–15 whales, still in pairs or triplets, that after 10 minutes had resumed their feeding activities 0.5 km from the killer whales incident.

Discussion

It appears that marine mammals are successfully attacked and eaten mainly by the larger, usually adult male killer whales (Nishiwaki and Handa 1958; Hancock 1965; Rice 1968; Jonsgård and Lyshoel 1970; Tarpy 1979). Apparently, most attacks on baleen whales, where only females or immature killer whales participate, are unsuccessful (e.g., Morejohn 1968; Cummings et al. 1972; this paper).

As demonstrated by several literature reports on killer whale predatory activities (Martinez and Klinghammer 1970; Steiner et al. 1979; Tarpy 1979; Smith et al. 1981), their hunting techniques are characterized by highly developed group coordination. It appears that those attacks involving immature killer whales, in some cases calves (Baldridge 1972; Cummings et al. 1972), are part of a complex learning behavior in which individuals increase and strengthen their individual and group hunting capabilities (described for pinniped hunting by López and López 1985).

Furthermore, Jonsgård (1968) concluded that, under "normal" conditions, it is very difficult for killer whales to kill baleen whales and other large cetaceans that are in good health. He based his conclusions on the absence of such reports during many years of Norwegian whaling in the northeastern North Atlantic. Several authors have provided evidence, in some cases circumstantial, to support Jonsgård's hypothesis, and it is not surprising that most of these observations have to deal with those relatively more accessible coastal species of baleen whales. For example, Andrews (1914) indicated that many gray whales taken commercially were found to survive killer whale attacks, as evidenced by damaged tongues, flippers, and other parts of the body. Rice and Wolman (1971) reported that 57 (18%) of 316 gray whales collected in California under scientific permit, showed evidence of having been attacked by killer whales (e.g., tooth marks on flukes and flippers), and concluded that this indicates a fairly high frequency of unsuccessful attacks. Morejohn (1968) observed an unsuccessful attack by seven killer whales on three gray whales, including a female with a calf. Cummings et al. (1972) described the unsuccessful attack of five killer whales on two southern right whales, ending after 25 minutes with no signs of blood or other evidence of physical harm. As pointed out by Jonsgård (1968), the attack on a minke whale reported by Hancock (1965), was on an animal "trapped" by low tide in a small and shallow bay and was therefore an easy prey. The blue whale wounded off Baja California, México, (Tarpy 1979) was immature and was attacked by about 30 killer whales (including several mature males). Our observation on the apparently unsuccessful attack on fin whales provides additional evidence to support Jonsgård's (1968) conclusion.

Observations on at least three species of cetaceans known to be preyed upon by killer whales, gray whales, humpback whales, and white whales, *Delphinapterus leucas*, show that they sometimes remain completely motionless in the presence of killer whales (Kellogg 1940; Hubbs 1965; Tomilin 1967; Baldridge 1972), probably in order to avoid detection. After a series of underwater sound playback experiments, Cummings and Thompson (1971) concluded that gray whales recognize the voice of killer whales, that they can easily localize the sounds underwater, and that they flee killer whale vocalizations. Such avoidance, according to these researchers, involves several behaviors, e.g., sound localization, silence, and reduced exposure (including invisible and non-audible blows), that appear to function as protective mechanisms. Similar underwater acoustical experiments carried out by Fish and Vania (1971) with white whales showed similar protective responses in the presence of killer whales sounds.

As noted previously, while the three killer whales were harassing the pair of fin whales, at least six high whistling sounds were audible. These killer whale sounds possibly correspond to the "whistles" (tonal vocalizations) or "screams" (pulsed vocalizations) recorded during cooperative feeding behavior by Steiner et al. (1979). We apparently detected the killer whales visually before the pair of fin whales were aware of them, and possibly the killer whales were silent before the attack in order to avoid detection.

Acknowledgments

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    Relationship between fish culture methods and pondwater quality in freshwater fish culture. By Kenji Chiba. Pages 1–7, 1 fig., 5 tables.

    Environmental management of larval rearing of marine fishes—A short history of research to prevent lordosis in red sea bream, *Pagrus major*. By Kunihiko Fukusho and Chikara Kitajima. Pages 9–13, 3 figs.

    Salinity tolerances of marine bivalves. By Shoji Funakoshi, Tohru Suzuki, and Koji Wada. Pages 15–18, 1 fig., 1 table.

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    Molecular toxicology: A new frontier. By Thomas T. Chen, Rebecca J. Van Beneden, Luis B. Agellon, Duane A. Howard, and Ronald A. Sonstegard. Pages 9–14, 4 figs., 1 table.

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    Juvenile hormone in Crustacea. By Hans Laufer, David Borst, Fred C. Baker, and David A. Schooley. [Abstr.] Page 39.

    Recent advances in nursery culture of bivalve mollusks in North America. By John J. Manzi and Nancy H. Hadley. Pages 41–46, 3 figs., 5 tables.

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    Sowing culture of scallop in Japan. By Hiroshi Ito. Pages 63–69, 7 figs., 1 table.

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FISHERY BULLETIN

VOL. 87, NO. 3 JULY 1989

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The *Fishery Bulletin* carries original research reports and technical notes on investigations in fishery science, engineering, and economics. The Bulletin of the United States Fish Commission was begun in 1881; it became the Bulletin of the Bureau of Fisheries in 1904 and the Fishery Bulletin of the Fish and Wildlife Service in 1941. Separates were issued as documents through volume 46; the last document was No. 1103. Beginning with volume 47 in 1931 and continuing through volume 62 in 1963, each separate appeared as a numbered bulletin. A new system began in 1963 with volume 63 in which papers are bound together in a single issue of the bulletin instead of being issued individually. Beginning with volume 70, number 1, January 1972, the *Fishery Bulletin* became a periodical, issued quarterly. It is available free in limited numbers to libraries, research institutions, State and Federal agencies, and in exchange for other scientific publications.

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Reuben Lasker:
A REMEMBRANCE
1929 - 1988

THIS ISSUE OF THE Fishery Bulletin *is in memory of Dr. Reuben Lasker who, until his death, was Chief of the Coastal Fisheries Division of the Southwest Fisheries Center, National Marine Fisheries Service. The contributors and I feel both a debt of gratitude and a strong bond of friendship to this scientist who profoundly influenced our investigations, our careers, and the field of marine larval ecology. Our regret is that Reuben will not see this tribute.*

Andrew E. Dizon, Ph.D.
Scientific Editor

It is the spring of 1989 in La Jolla, California, almost a year since our friend and colleague, Reuben Lasker, left us after a valiant battle against cancer. We remember him fondly, with respect and admiration for the man and for the scientist whose intellectual honesty and humanity endeared him to his associates. We, therefore, dedicate this Festschrift to the memory of a remarkable human being, a warm and caring man, who combined a lifelong passion and dedication to the marine sciences with a bright intelligence, a lively curiosity, and an abiding appreciation of the world around us.

Reuben was born in Brooklyn, New York, December 1, 1929, the only child of Theodore and Mary Lasker. As a child he contracted rheumatic fever, and as was customary at that time his doctors prescribed bed rest for an extended period, when Reuben read avidly. The illness, which left Reuben with a slight heart murmur, influenced his activities and increasingly the boy turned to bookish pursuits. He did well in school, attending the prestigious Boys' High School in Brooklyn, graduating at 16. Because of his health, his father decided that Reuben should go to college in Miami, Florida, to escape the rigors of the severe winters in New York. Accordingly, in 1946, Reuben enrolled at the University of Miami as an English major.

Midway through his college career, Reuben switched his major to zoology with the thought of becoming a medical doctor and in fact actually served as president of the premed society. He received his B.S. degree with honors in zoology, with a minor in chemistry, from the University in 1950. When a graduate research fellowship became available in marine biology, Reuben made a fateful career decision to abandon medicine and applied for the post. He was awarded a full tuition scholarship with stipend for studies in marine biology at the University of Miami where he concentrated on studies on the physiology and cellulose digestion in the shipworm, *Teredo*. He was granted his M.S. in marine biology from the University of Miami in 1952.

Approaching the end of his fellowship at Miami, Reuben began to investigate options for continuing his graduate education. He corresponded with the physiologist, Professor Arthur C. Giese of Stanford University, who had an ongoing marine program at the Hopkins Marine Station. With Giese's encouragement Reuben applied for and was granted a predoctoral fellowship from the National Institute of Health for his doctoral studies at Stanford University. Initially, Reuben was given a small stipend to study the nutrition of the plentiful sea urchins around Monterey Bay. With his young wife, the former Caroline Hayman, the couple drove west in their 1941 black Ford sedan.

Reuben spent the years from 1952 to 1956 on the Stanford campus in Palo Alto researching and writing his doctoral thesis on cellulose digestion in the silverfish. He picked his doctoral topic by chance, although he believed in Pasteur's maxim that chance favors the prepared mind. As Reuben

Opp. page, left: Dr. Gotthilf Hempel of West Germany took this relaxed picture of Reuben during a visit to his laboratory in Building T-21 on the Scripps campus in 1963.

Opp. page, right: Examining a 1 m CalCOFI plankton net in 1965 on the deck of the Bureau of Commercial Fisheries research vessel, *Black Douglas*.

Right: Reuben receiving the U.S. Department of the Interior Silver Medal in 1970 as Gerald V. Howard, Regional Director of the Southwest Region and Alan R. Longhurst, Director of the Fishery-Oceanography Center look on.

was fond of telling the story, he was sitting in a gloomy roomette where the only object left by the former occupant of the cubicle was a box of tissues used in laboratory work. When he reached over and pulled one out, an insect fell down to the table top, skittered away, fell to the floor and disappeared into a crack. The tissue was full of holes and he realized that what he had seen was a silverfish who had made a meal of the paper. Cellulose is difficult to digest by most organisms, and the conventional thought was that animals that eat cellulose, such as the cow or termites, have microorganisms in their stomachs to do the digesting for them. Reuben reflected that since no one had ever mentioned how a silverfish did its cellulose digesting, this might be a suitable topic for a Ph.D. thesis. On completion, the thesis was ranked "Superior" by Stanford University and established Reuben's reputation as an authority on the physiology of this insect. He received his Ph.D. degree in biology in 1956.

In February 1956, Science magazine carried a small announcement in its back pages that a meeting, sponsored by the Rockefeller Foundation, was to be held at the Scripps Institution of Oceanography in La Jolla, California on the future of marine biology. A small amount of money had been set aside for graduate students who were asked to apply to Dr. Adriano Buzzati, the convenor. Reuben promptly wrote to Buzzati, explaining that he was a graduate student at Stanford in marine biology and eminently qualified by inclination and interest to attend. By return mail he received a round-trip ticket from Palo Alto to San Diego and a check for $50 "to cover expenses." At the train station in San Diego, Reuben was picked up by Leo Berner, then a graduate student at Scripps and presently a professor and former dean of oceanography at Texas A&M University, who later became a close friend.

Famous names in marine biology were in attendance at the meeting—Albert Szent-Gyorgyi, Nobel Laureate for the discovery of vitamin C; the English biochemist Ernest Baldwin; Eugene Odum, ecologist from the University of Georgia; Roger Revelle, then the Director of the Scripps Institution of Oceanography and later one of the founders of the University of California, San Diego; John Isaacs, professor of oceanography who was destined to have a profound influence on Reuben; and many others who collectively represented the forefront of research in marine biology, worldwide.

Buzzati, a geneticist, was then a professor at Scripps. He offered to submit a proposal for Reuben to the Rockefeller Foundation to culture euphausiid shrimps, a project on which Reuben had been working. On his return to Stanford, Reuben wrote the proposal and by return mail received notice that he had been awarded a post-doctoral appointment for $5,000 a year (tax-free). By the following September, Reuben and Caroline arrived in La Jolla in a car packed with all their possessions.

The project Reuben chose for himself was to attempt to maintain euphausiids in reasonable health in the laboratory and to find out how effi-

Reuben with Walterio Garcia, Jacobo Melcer, and Paul E. Smith aboard the research vessel *A. Humboldt* in 1975.

Opp. page, left: In foul weather gear aboard the University of Alaska's research vessel, *Alpha Helix*, during a research cruise to the Pribilofs in 1982 to study groundfish.

Opp. page, right: Showing off the Huntsman Medal for Excellence in Biological Oceanography awarded him in 1983 by the Canadian government's Bedford Institute of Oceanography.

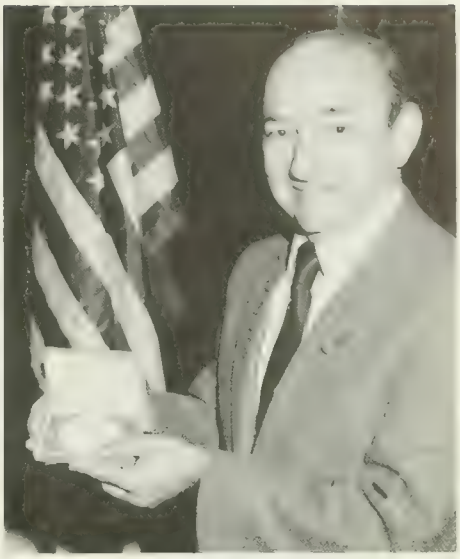
ciently they used their food. Since no one offered to provide him with live animals to work on, Reuben arranged to go to sea on the Scripps T-boat (the U.S. Army's designation for Transportation), an 80-foot vessel with a 3-man crew. Dosed massively with Dramamine, the former Brooklynite who never learned to swim, was taught how to catch euphausiids by Scripps researchers Elizabeth and Brian Boden. During one particularly eventful trip, Reuben was 10 miles off San Diego where the vessel had been stopped to deploy a plankton net. Alone on deck, in heavy seas and without a life jacket, Reuben remembered the ship giving a sudden lurch that propelled him forward over the chain railing. Fortunately for Reuben he managed to save himself by grabbing a projecting object as the ship steamed ahead at 10 knots away from where he would have been hurled into the sea.

Until he finally figured out the correct dosage of Dramamine, Reuben was very susceptible to sea sickness. Although it was necessary to go to sea to collect live specimens, Reuben preferred to keep his sea trips as brief as possible. Serendipitously, he located an area of the ocean in the lee of Pt. Loma which not only produced euphausiids and fish larvae in abundance but also had the virtue of being relatively calm. This became his favorite spot for collecting specimens and in years to come became well known to his colleagues as Lasker's Lake.

The postdoctoral year went quickly with Reuben who was working on the energy balance of euphausiids and looking for a job. A notable event for the Laskers during this time was the birth of their daughter, Pamela.

It was also during Reuben's sojourn at Scripps that a meeting took place which had important implications for his future. Through a mutual friend he met John C. Marr, Director of the U.S. Department of the Interior's Bureau of Commercial Fisheries, South Pacific Fisheries Investigation, who had recently relocated his laboratory in the old Director's residence on the Scripps campus. Marr was interested in Reuben's work on euphausiids, and some months later when the laboratory was reorganized he asked Reuben to head up a physiology section. Meanwhile, Reuben had accepted a job at Compton Junior College; although it provided him with his first taste of teaching, he informed the dean that he would not be renewing his contract because he wanted to return to research. At the end of the academic year, the Lasker family left Compton and returned to La Jolla, where Reuben had been granted a Lalor Faculty Fellowship at the Scripps Institution of Oceanography. In the interim Marr was able to complete the arrangements for Reuben's recruitment. Accordingly, in June 1958, Reuben entered on duty at the federal fisheries laboratory in La Jolla, as a fishery research biologist. Thus began a creative, productive partnership, an association that lasted through numerous federal reorganizations and changes in research emphases, and which endured until Reuben's death some 30 years later.

In establishing a Physiology Program and



selecting Reuben as its principal investigator, Marr embarked on a major change in the direction of research on pelagic marine fishes. He believed that there were many problems that could be solved only through controlled laboratory experiments. Heretofore, few studies had been made on the physiology of pelagic fishes. It had not been possible, for example, to study the fecundity of sardines and other pelagic fishes under laboratory conditions, since fish held in aquaria were not known to spawn. However, under proper conditions of diet or by control of endocrine development, it was at least theoretically possible to induce normal spawning in aquaria. Marr proposed that Reuben undertake such studies as the investigation of the efficiency of food utilization by larval fish, the influence of various factors on the rate of growth, the change in body conditon during ovarian development, and the like.

With this as a mandate, Reuben moved into T-21, one of the gray clapboard cottages (former residences of Scripps' professors) that dotted the hills around Scripps Institution of Oceanography. With the help of his newly hired assistant, Gail Theilacker, a former graduate student at Scripps, he proceeded to establish a laboratory oriented toward basic research, whose main purpose was the study of the innate and adaptive responses of marine organisms. Although Reuben's main academic interest was the investigation of energy exchanges between marine animals and their food supply, he was also interested in other physiological functions that could affect an organism's ability to survive in the sea.

The Physiology Laboratory in T-21 whirred with activity as Reuben threw himself into his new job, infecting others with his customary energy and enthusiasm. Soon, old white bathtubs with clawed feet were filled with seawater and located inside and outside T-21 to hold experimental animals. A particularly robust colony of brine shrimp and algae flourished as a self-contained ecosystem in yet another outside bathtub. One of the first high-speed Beckman ultracentrifuges, used to separate different sardine proteins, hummed upstairs. In another room a continuous oxygen measurement system, using one of the first double electrode probes, which had been invented by Reuben's close friend and colleague, Dr. John Kanwisher, of the Woods Hole Oceanographic Institution, produced quantities of exciting data.

Because government funds were scarce, Reuben took every opportunity to take advantage of federal government surplus property to equip his laboratory for experiments on respiration and energy uptake of sardine eggs and larvae. In the absence of a proper cold room, he located a meat packer's cold locker and set this up outside the building. Another piece of equipment picked up from government surplus lists was a hot dog cooker that had small, rotating aluminum rods to heat the wieners. This, minus the heating element, was adapted by Reuben and Gail to turn syringes

filled with sardine eggs rather than wieners. In his enthusiasm to properly study respiration in sardine eggs directly from the sea, Reuben and Gail even installed their Warburg respirometer, without the cooling and shaking system, on the Bureau's old research vessel, the *Black Douglas*, reasoning that the continual shaking motion of the ship would adequately mix the eggs with seawater. Since the work required a constant cold temperature, the only location that met the requirement aboard the *Black Douglas* was deep within the bowels of the ship, accessible only by crawling into the confined space on hands and knees.

It was also about this time that the Cahn electrobalance, now a staple of well-equipped laboratories was developed. The inventor himself set up the equipment in Reuben's T-21 where it was used for weighing individual sardine eggs and larvae. Reuben also took pride that he was one of the first scientists to use the carbon-hydrogen-nitrogen analyzer, and in fact field tested it for the company manufacturing the equipment.

The laboratory soon became a magnet for visiting scientists, investigators, and graduate students. During the summer months, high school students labored at various tasks, measuring euphausiid lengths, collecting limpets, and extracting substances from the tube feet of starfish. From his vantage point at a large wooden desk before a picture window with the panorama of the California coastline curling north, Reuben supervised this activity, while continuing to author or co-author numerous papers on energetics of euphausiids, energetics of sardines, physiology and ecology of fish larvae, and ultimately to studies of the mechanisms underlying recruitment of fishes.

In 1963, Reuben organized a symposium on larval fish biology that would encompass topics ranging from systematics of fish larvae to the technology of fish rearing to the basic physiology of single fish eggs and larvae. In the process Reuben forged close personal and professional links with many of the scientists who attended—James Shelbourne of the Fisheries Laboratory in Lowestoft, England; Gotthilf Hempel of the Institut für Hydrobiologie of the University of Hamburg; J. H. S. Blaxter and F. G. T. Holliday of Aberdeen University; and others—associations which continued throughout his life.

In 1966, Reuben and his family, which now also included a son, Paul, traveled to Aberdeen, Scotland to work at the University of Aberdeen for one year with Blaxter and Holliday. Here Reuben applied the techniques perfected in his work on euphausiid shrimps to the study of the food chain in an experimentally developed fishery, utilizing hatchery-reared larval and juvenile plaice. The year in Scotland with his family proved to be one of the happiest in Reuben's life, leaving him with an abiding affection for all things Scottish.

In October 1964, the Bureau of Commercial Fisheries, Fishery-Oceanography Center, as it was then called, was completed, adjacent to the campus of the Scripps Institution of Oceanography. It was an imposing structure of four concrete buildings grouped around a central courtyard, 220 feet above the Pacific Ocean. The gray cottage, T-21, site of many research accomplishments, was abandoned. Reuben and his staff moved into a wing of the Center which was equipped with the most modern equipment and perhaps most importantly gave access to an experimental seawater aquarium with temperature control rooms for physiological studies and rearing experiments, all of which Reuben helped to design.

With the move into his well-equipped new laboratory, Reuben assembled a dedicated cadre of behaviorists, physiologists, oceanographers, population dynamicists, and experimental biologists. At this point in his professional life he had already established a solid basis of scientific achievement on which others could build. His work on the energy exchange between fishes and their food supply, his work on osmoregulation by sardine embryos and larvae, and his work on the effect of temperature on the growth and development of both sardine and anchovy larvae were fundamental to understand the dynamics of fish populations and provided the scientific rationale for the project to rear pelagic marine fish in the laboratory. Subsequently, under Reuben's direction and leadership, more than 30 species of pelagic fishes, including the commercially valuable sardine, anchovy, and mackerels, were reared from eggs, through larvae, to subadult stages, for the first time ever in a laboratory. Reuben's papers on marine invertebrates and on the energy budget of clupeids in relation to their planktonic food were widely read and quoted. His

paper on the feeding, growth, respiration, and carbon utilization of a euphausiid crustacean became a citation classic (Current Contents, 1983, Volume 14, page 17).

With outstanding researchers and equipment, particularly the facilities of the experimental seawater aquarium, at his disposal, Reuben was able to concentrate his research on ecological and physiological factors that would help answer one of the most important and fundamental questions in fisheries: What determines how many young fish will survive the rigors of life in the sea to become reproducing adults?

Ever the creative and imaginative scientist, Reuben constantly came up with fresh and innovative scientific approaches. An example was an experiment in which he took anchovy larvae spawned in the Center's seawater aquarium to sea in order to test his idea that laboratory-raised anchovy could be used in lieu of naturally spawned larvae as an assay of conditions in the sea.

Another remarkable idea came to Reuben when he was on a cruise to sample patches of larval food. Following a storm with strong winds that mixed and diluted the dense layer of larval forage from which he had drawn his samples, it occurred to him that upwelling events and storms are detrimental to fish larvae because these events dilute concentrations of larval food. He suggested that larval survival increases during periods of weak winds when the coastal seas stratify and the forage of larval fishes concentrates in layers. This "stability" hypothesis has greatly interested oceanographers and fishery biologists both in this country and abroad and has stimulated efforts of individual researchers to study the definitive links between fish larvae and their microenvironment. Now known as "Lasker Events" (see following article on "An eponym for Reuben Lasker" by Daniel Pauly), these calm periods could be the key factor in larval survival, and ultimately recruitment.

The years passed quickly and happily for Reuben. As Chief Scientist of what would become the Coastal Fisheries Resources Division, he directed the efforts of a multidisciplinary research team and was signally successful in stimulating and inspiring his staff to pursue promising avenues of research. This record of research achievement received mention in the review conducted by the National Academy of Sciences in its evaluation of the National Oceanic and Atmospheric Administration's ocean research and development. The examiners wrote, "The Coastal Division represents a center of excellence . . . the Division has a high scientific awareness, much talent and enthusiasm, and is doing some excellent research."

One remarkable example of how Reuben's leadership and influence led to a major breakthrough is his role in developing the estimation procedure for anchovy biomass assessment. He was among the first to recognize the unique potential of this method and was responsible for bringing together the disparate disciplines and people that made it work. The method permits the estimate of biomass from the ratio of the egg production rate in the sea to the daily fecundity of the spawning fish stock. This new method of pelagic population analyses was accomplished by a team effort and was founded almost entirely on previous research done by Reuben and others, research which provided the essential background information on which to build. In order to develop the anchovy biomass assessment, a wide variety of studies on sampling, statistical methodology, fish biology, ecology, behavior, and physiology had to be made. All of these studies added greatly to the knowledge of clupeoid biology.

As of this writing, the biomass assessment method has been incorporated into the Northern Anchovy Management Plan as a guide for setting anchovy fishing quotas in the coastal waters of the U.S. Pacific Coast and has been adapted in other countries such as South Africa and Peru. It is increasingly viewed by many fisheries scientists as the best current assessment technique for fishes with pelagic eggs.

In 1970, in response to a request from the administrators of the fisheries service, Reuben (with the able assistance of the late Lon Manar as the managing editor) undertook the task, as scientific editor, of revitalizing the venerable U.S. *Fishery Bulletin.* Before 1971, the Fishery Bulletin appeared irregularly for lack of sufficient contributions of merit. Authors sought other journals because it took 2–3 years to get papers published in the Fishery Bulletin. During Reuben's first year as editor, the Fishery Bulletin became a quarterly and the number of pages printed per year almost tripled. Be-

cause of his scientific reputation, Reuben was able to attract to the pages of the Fishery Bulletin not only outstanding contributions from members of the NMFS staff but also major contributions from scientists outside NMFS. He initiated and enforced a peer review system for reviewing manuscripts, not only for the Fishery Bulletin but also for other NMFS publications. His impact on the scientific image, character, and tone projected by NMFS publications was a reflection of his own standards of scientific excellence and personal integrity. The revitalized Fishery Bulletin, an indispensable research journal to those in the field of fisheries, now reaches several thousands of readers worldwide. Reuben's contributions as Scientific Editor were even more remarkable becaues he worked at this job only half-time while continuing his research on fish physiology.

Reuben also served as an essential link to the surrounding academic community, particularly the nearby Scripps Institution of Oceanography with which the fisheries laboratory had long maintained close ties. In 1966 he received an appointment as an Associate Professor of Marine Biology in Residence at Scripps and in 1973 was appointed Adjunct Professor of Marine Biology. He supported and encouraged his graduate students, and participated with his usual enthusiasm in faculty committee work. It was most typical of Reuben that although his strength was sapped by his illness he introduced his last graduate student at a thesis defense several days before his death with humor and wit.

During his 30 years as a government scientist he put together many workshops and meetings which attracted scientists from all over the world and fostered creative collaborative efforts. For example, in recent years, he organized workshops for the Sardine-Anchovy Recruitment Program (SARP) which brought together scientists from all major upwelling regions of the world to develop a practical plan for studying recruitment. Major credit for the active and productive SARP programs that exist today in many parts of the world belongs to Reuben's efforts and interest.

He was a gregarious man who loved people and conversation. He delighted in travel to the far places of the world. Many of the letters received after his death testify eloquently to the warm affection and regard in which he was held by hundreds of his colleagues throughout the world.

During his lifetime Reuben was the recipient of high honors. The U.S. Government awarded him the Meritorious Service Award of the U.S. Department of the Interior (Silver Medal Award) in 1970 and the Distinguished Service Award of the U.S. Department of Commerce (Gold Medal Award) in 1974. The Canadian Government's Bedford Institute of Oceanography awarded him the Huntsman Medal for Excellence in Biological Oceanography in 1983.

Reuben's preeminent role as outstanding researcher, his practical wisdom, wide experience, and knowledge made him much sought after as a prime mover, advisor, and member of many prestigious committees, commissions, and boards where he served with distinction, most recently as a member of the Ocean Studies Board of the National Academy of Sciences.

He maintained close ties with friends and colleagues around the world, through voluminous correspondence and telephone calls. He was ever the optimist and many of his correspondents never realized the gravity of his illness which re-occurred in March of 1987. As his lifelong close friend, Dr. Howard Feder of the University of Alaska wrote later, "I can hear Reuben's voice in my head saying, 'Goodbye, old buddy. Don't be sad. I did everything I wanted; I have no regrets. Remember, Howie, life goes on! Enjoy yourself.'" On April 27, 1988 his friends scattered his ashes from the National Marine Fisheries Service research vessel, *David Starr Jordan*, appropriately enough, in the sea off Point Loma, known as Lasker's Lake.

For those of us lucky enough to have shared this life with him, the thought of Reuben will always bring the warmest memories. As his friend Lucian Sprague wrote, "As long as there are friends who remember him, students to read his papers and to carry on his work, he will be very much with us in spirit."

In the year which followed Reuben's death, his friends organized the Reuben Lasker Memorial Fund. The Fund is administered by the Coordinator of the California Cooperative Oceanic Fisheries Committee (CalCOFI) and is used for travel fellowships for students to attend the annual CalCOFI meeting. Anyone interested in contributing to the

fund may do so by writing to the CalCOFI Coordinator, P.O. Box 271, La Jolla, CA 92038. Also in 1988, the American Institute of Fishery Research Biologists posthumously awarded Reuben their Outstanding Achievement Award for his distinguished lifetime career accomplishments in fisheries science and for his outstanding contributions to research and management.

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An Eponym for Reuben Lasker

Reuben Lasker published in 1975 and 1978 two papers in which he suggested that the maintenance—through a "period of calm"—of thin layers of food-rich patches was crucial to the survival of newly hatched northern anchovy larvae. These papers had an enormous influence on fisheries research throughout the 1980s, as can be easily assessed, e.g., through citation analysis.

Recently, Peterman and Bradford (1987, their note No. 16) operationally defined the periods of calm alluded to above as periods of four consecutive days with wind speed below 10 m s^{-1}. They also proposed to view periods of five consecutive calm days as two partly overlapping 4-day periods, period of six days as three partly overlapping periods, etc.

I recently proposed (Pauly 1987), in a book largely devoted to following up on R. Lasker's work, the term "Lasker events" as an eponym for a period of four calm days with winds less than 5 m s^{-1}. The present volume provides an appropriate context to reiterate and refine this suggestion.

Thus, to allow different authors to identify different hypotheses related to the effects of periods of calm, I propose to use the notation "*i/j* Lasker event" for period of calm lasting *i* days and defined by winds not exceeding *j* m s^{-1}. Thus, e.g., Peterman and Bradford (1987) worked with "4/10 Lasker events", while Mendelssohn and Mendo (1987) worked with "4/5 Lasker events".

This suggestion offers a parallel for the more general "Lasker-hypothesis" now widely used as an eponym for the mechanism proposed by Lasker (1978, 1985).

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Optimal Wind Conditions for the Survival of Larval Northern Anchovy, *Engraulis mordax*: A Modeling Investigation

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ABSTRACT: How the frequency of storm events can influence the survival of larval northern anchovy, *Engraulis mordax*, was investigated by computer modeling. The hypothesis was as follows. While wind events dissipate layers of planktonic food, a total absence of wind mixing would reduce upward nutrient flux and retard plankton production. Therefore, there must be optimal conditions of wind speed, duration, and frequency of wind events for maximum survival of northern anchovy larvae. From numerical experimentation, all wind events were detrimental to post-yolk-sac larvae present in the water column at the time of the storm. However, if initial prey concentrations are insufficient for optimal growth of larvae, then a wind event which increases primary and secondary production may be beneficial to larvae emerging from the yolk-sac stage after the storm. The conclusion was that optimal conditions for larvae survival occur when a wind event strong enough to deepen the mixed layer into the nutricline is followed by a period of calm. This period between storms must be long enough for larvae to develop into a stage where short-term starvation can be endured.

In 1975, Lasker hypothesized that larval anchovy survival was dependent on the stability of the water column. Laboratory work (see Blaxter and Hunter 1982; and references therein) showed that first-feeding anchovy require very high concentrations of plankton food. These high concentrations are found in the upper water column, but only during periods of low winds and reduced turbulence (Lasker 1975; Owen 1989). Recently Peterman and Bradford (1987) performed a statistical analysis of wind and larva mortality data from the field that confirms Lasker's hypothesis. There is a statistically significant relation between larva mortality rate and the frequency of calm, low wind speed periods which permit the maintenance of concentrated patches of food.

However, completely calm wind conditions cannot be ideal, because a stratified water column reduces the vertical flux of nutrients into the euphotic zone, reducing production of plankton (Lewis et al. 1986). Eppley and Renger (1988) recently measured the slight increase in nitrate in the surface layer owing to a moderate wind event in California coastal waters, and found the data consistent with the wind driven, nutrient flux dynamics of Klein and Coste (1984).

Consider the fact that northern anchovy, *Engraulis mordax*, populations off central and southern California spawn mostly during the winter and spring months (Smith 1972; Smith and Richardson 1977), not during the summer when winds are most calm and the water column most stratified by solar heating (Husby and Nelson 1982). The timing of the spawning of these populations may be an adaptation to maximize the survival of larvae.

This is the third in a series of modeling efforts (Wroblewski 1984; Wroblewski and Richman 1987) to simulate the environmental conditions which influence the survival of northern anchovy. Each successive model builds on the previous model by increasing complexity (and realism) in the biological and physical dynamics. Here we investigate by numerical experimentation the manner in which the frequency of storms during the spawning season of northern anchovy could influence survival of larvae. We find there is indeed a theoretical optimum condition of wind speed, duration of event, and frequency of events for maximum survival.

METHODS

Our model investigates the mortality of north-

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ern anchovy larvae for 15 days from first feeding. From histological indications of tissue condition, O'Connell (1980) showed that anchovy larvae less than 10 mm SL are vulnerable to starvation. For northern anchovy, yolk-sac absorption and first feeding occurs 3 to 4 days (depending on temperature) after egg hatching. Larvae obtain a standard length of 10 mm about 19 days after hatching (Blaxter and Hunter 1982). Thus the larvae are subject to starvation for 15 days after first feeding. The larvae metamorphose at 34 to 40 mm SL, about 56 to 60 days after hatching.

O'Connell (1980) suggested that larvae above 10 mm SL may be less vulnerable to starvation because of increasing nutriment (protein, carbohydrate, and lipid) reserves with growth. Early post-yolk-sac larvae have negligible reserves and will survive only two or three days without any food (Lasker et al. 1970; O'Connell and Raymond 1970). Larger (35 mm SL) larvae can survive two weeks of starvation as their lipid content declines (Hunter 1977).

Because of their small mouth size, first-feeding northern anchovy larvae are restricted to feeding on small prey (Hunter 1977). First-feeding northern anchovy are initially able to subsist on a diet of the unarmored dinoflagellate *Gymnodinium splendens* (Lasker et al. 1970). However, after a few days, their growth rate will be greatly depressed unless their diet includes more typical foods of young clupeoid larvae such as tintinnids, ciliates, copepod eggs, naupliar, and copepodite stages (Arthur 1976; Blaxter and Hunter 1982; Theilacker 1987). Therefore, in our model, we consider the prey of young anchovy larvae to be microzooplankton. We do discuss later the availability of *G. splendens* to first-feeding larvae under the turbulent mixing conditions predicted by the model.

Larval Fish Dynamics

Our formulation of growth and mortality of larval northern anchovy (see Wroblewski 1984) is based on the laboratory experiments of O'Connell and Raymond (1970), who determined the effect of various zooplankton prey concentrations on the survival of larvae over the first 12 days of life. The prey in the O'Connell and Raymond (1970) experiments were wild crustacean nauplii with some tintinnids and phytoplankton also present.

The equation for growth rate of larval anchovy expresses the difference between metabolic gains and losses,

$$\text{growth} = \text{ingestion} - \text{egestion and excretion}.$$

Ingestion of prey by larval anchovy is calculated, using the Ivlev (1955) formulation for the feeding of fishes. Egestion of fecal matter by anchovy larvae is taken to be a constant fraction of the ingested ration. Metabolic excretion is assumed to occur at a basal rate plus an additional excretion associated with feeding activity.

Larval anchovy mortality is expressed in the model as a function of weight at age, or in other words, the feeding history of the larvae,

$$\text{mortality} = \text{baseline growth rate/actual growth rate}.$$

Mathematical formulations for larval anchovy growth and mortality used here are the same as equations (5) and (6) in Wroblewski and Richman (1987).

Prey Dynamics

The equation for the concentration and vertical distribution of the prey of larval anchovy (microzooplankton) is one of a set of coupled partial differential equations describing the plankton ecosystem. These equations for phytoplankton, zooplankton, and dissolved nutrient (nitrate) in a one-dimensional water column are given as equations (1) to (4) in Wroblewski and Richman (1987). Analytical solutions to these plankton equations have been derived and sensitivity analyses have been performed so that one can fully understand how the concentration of prey responds to changes in the biological parameter values (see Franks et al. 1986; Wroblewski and Richman 1987).

The biological parameter values used here are the same as in table I of Wroblewski and Richman (1987), with the exception that the growth rate of the phytoplankton is reduced. In the previous study, it was assumed that the average growth rate in the euphotic zone (waters with greater than 1% surface light intensity) was 2 doublings day^{-1}, if nutrients were not limiting. Here we assume that the maximal growth rate of the phytoplankton at the surface is 2 d^{-1}. Below the surface, the growth rate of the plants is given by $V = V_m \exp(-k\,z)$, where V_m is 2 d^{-1} and the light extinction coefficient k is 0.1 m^{-1}. The effect of this change in plant growth rate is to reduce the concentration

of phytoplankton in the water column, so that the simulated profile of phytoplankton (Fig. 1a) more closely resembles the observations off Southern California reported in Cullen et al. (1983) and Mullin et al. (1985).

The modeling studies by Wroblewski (1984) and Wroblewski and Richman (1987) examined how the concentration of prey responds to perturbations in the physical oceanographic environment caused by wind forcing. Wroblewski (1984) used scale analysis to deduce the thickness of the layer of prey which could be maintained during wind-induced turbulent mixing. He found that the effectiveness of turbulence in dispersing food for northern anchovy larvae is lowered by any ability of the prey to aggregate into patches. The conclusion was that first-feeding larvae could find sufficient concentrations of motile *G. splendens* in the pycnocline during moderate wind conditions.

Wroblewski and Richman (1987) coupled the plankton equations to a simplified model of mixed layer dynamics (Niiler 1975) to calculate wind-driven deepening of the mixed layer and the turbulent diffusivity within the mixed layer during and after a wind event. Wroblewski and Richman found that wind events are always detrimental to larval northern anchovy, because wind mixing dissipates vertical structure in prey concentration as Lasker (1975) proposed. However, they discovered that interacting biological and physical processes determine the time interval before high concentrations of prey are reestablished, i.e., the starvation period endured by the anchovy larvae. Reproduction by prey and their aggregation by swimming govern the rate of reestablishment of vertical structure in prey distributions, once wind conditions allow turbulence in the upper water column to dissipate. They noted as significant that first-feeding larval anchovy forage directly on *G. splendens* and microzooplankton which have the reproductive capacity and migration ability to reestablish high concentrations shortly after a storm.

Wroblewski and Richman (1987) were able to quantify the influence of wind event magnitude and duration on larval northern anchovy survival. However, as Niiler's (1975) mixed layer model does not permit restratification of the upper water column by solar heating between wind events, more complex physics was required to explore the influence of interstorm duration on larval anchovy survival.

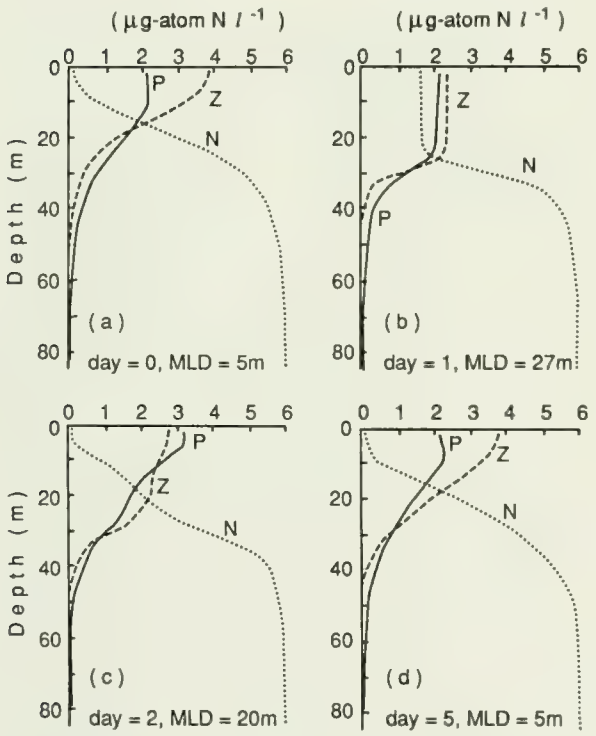

FIGURE 1.—Temporal evolution of the one-dimensional (vertical) plankton model in response to a single wind-mixing event. Initial conditions are the steady state profiles of phytoplankton (P), zooplankton (Z), and nitrate (N) shown in panel (a). The wind speed during the event is 16 m s^{-1} with 24 h duration. MLD refers to the mixed layer depth.

Mixed Layer Dynamics

Here we use the mixed layer dynamics of Mellor and Yamada (1974; 1982) which predict both wind-driven deepening of the mixed layer and shallowing of the mixed layer by solar heating. Heat is absorbed at the sea surface and shortwave radiation penetrates the surface, attenuating exponentially in the manner formulated by Simpson and Dickey (1981).

Klein and Coste (1984) used the turbulence closure scheme of Mellor and Yamada (1974) to study the influence of wind forcing on nutrient transport into the mixed layer, but treated nitrate as a conservative quantity. Chen et al. (1988) used Mellor and Yamada (1974) dynamics with both wind and tidal forcing to simulate vertical nutrient mixing in Long Island Sound, but also considered biological consumption and production of nitrate. We refer the reader to Klein and Coste (1984) and Chen et al. (1988) for details on the implementation of Mellor and Yamada's (1974) level 2.5 dynamics in this type of physical-biological modeling study.

Initial Conditions

The initial conditions for a simulation are the steady state solutions of the plankton dynamics for a stratified water column (Fig. 1a). The initial temperature gradient is 4°C over the upper 100 m. The daily average surface heating is 50 W m^{-2} which is divided equally between short- and long-wave radiation. A background eddy diffusivity of 10^{-4} m^2 s^{-1} throughout the water column is assumed.

RESULTS

Multiple Wind Events

Figure 2 shows the wind speed, level of turbulent mixing at 3 m below the surface, and the mixed layer depth for the simulation where three wind events occur within a 15 d period. Fifteen days is the critical period after yolk-sac absorption when northern anchovy larvae are susceptible to starvation (O'Connell 1980). Each wind event has a wind speed of 16 m s^{-1} and a duration of 24 hours. Between the events, the water column restratifies due to a solar heating of 25 W m^{-2} at the surface and to a short-wave radiation flux of an additional 25 W m^{-2} penetrating the upper 10 m of the water column.

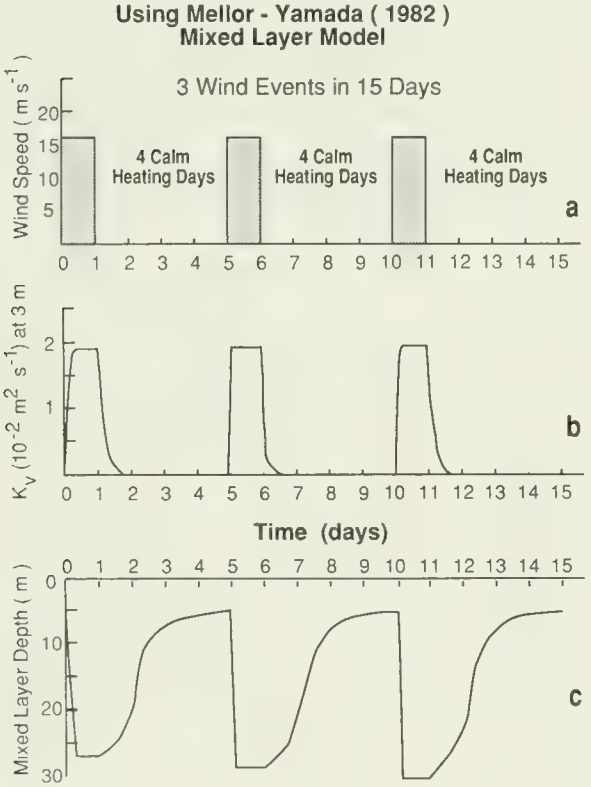

FIGURE 2.—The wind speed (a), vertical eddy diffusivity K_v at 3 m depth (b), and mixed layer depth (c) during a simulated 15 d period. The Mellor-Yamada (1982) model was used to calculate K_v and the mixed layer depth.

In the Mellor-Yamada (1982) model, the turbulent diffusion coefficient K_v is predicted as a function of depth; it has a maximum within the mixed layer and decreases markedly below. Since we are primarily concerned with dissipation of plankton near the surface where the concentration of prey is greatest (due to high productivity of the phytoplankton), we plot in Figure 2b the value of K_v at 3 m depth over the 15 d period. The deepening of the mixed layer during each event and its shallowing after each wind event is shown in Figure 2c. Note that the mixed layer deepens slightly more with each subsequent event, as the water column does not completely restratify during the 4 d period between each wind event. The background diffusivity maintains a mixed layer 5 m deep.

The model prediction of the increase in larval anchovy mortality for the three wind event case is shown as curve b in Figure 3. For comparison the mortality rate for larvae which experienced only a single event of the same wind speed and duration is shown as curve a in Figure 3. Curves a and b are the same until day 5 when the second wind event begins. The mortality rate for larvae experiencing a second and then third wind event continues to increase with time, while the mortality rate for larvae enduring only one event declines as turbulence in the water column dissipates and food concentrations are reestablished (see Figure 1, panels c and d).

The mortality rate after 15 days for larvae having endured a single wind event is about 6% d^{-1}. If no wind event had occurred, their mortality rate would be about 4% d^{-1} (curve e in Figure 3). Thus a single event does not have a great cumulative effect. However, for larvae having endured 3 wind events over their 15 d development period, the mortality rate increases to 13% d^{-1} (curve b in Figure 3).

The mortality rate increases dramatically with the frequency of wind events. Curve c in Figure 3 shows the influence of 5 wind events each of wind speed 16 m s^{-1} and 24 hours duration on a cohort of larvae reaching the first feeding stage at time zero. The mortality rate at the end of 15 days is 21% d^{-1}.

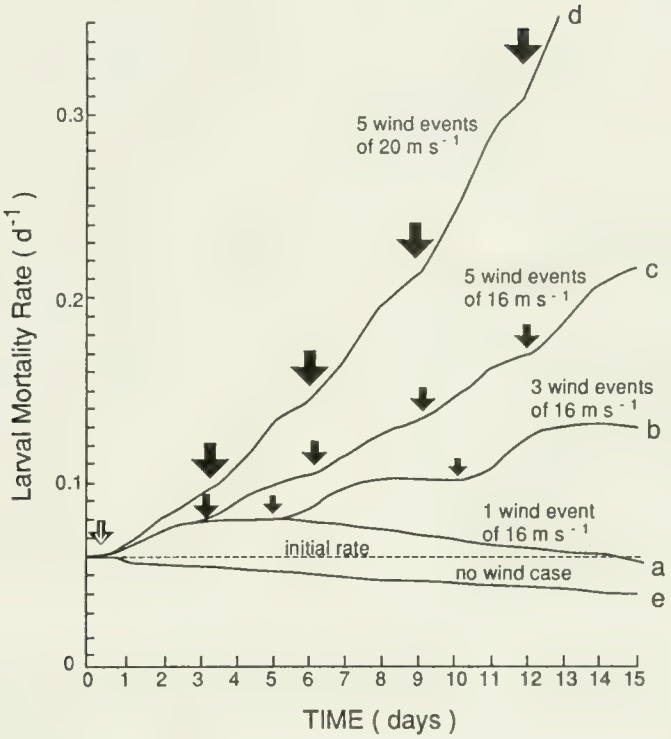

FIGURE 3.—Mortality rate predicted for larval northern anchovy positioned at 3 m depth in the water column (the depth of maximum growth and survival in the model water column). Curve a shows the predicted mortality rate for an event where the wind blows at 16 m s^{-1} for 24 hours. Curves b, c, and d show the mortality rate for larvae experiencing multiple wind events. Curve e gives the mortality rate where winds are calm during the simulated 15 d period. Day zero is the day of first feeding of a cohort of larvae. Arrows indicate the beginning of wind events.

The mortality rate also increases with the strength of the storms. For larvae enduring 5 wind events of 20 m s^{-1} wind speed, each lasting 24 hours, the mortality rate at day 13 is 35% d^{-1} and 45% at day 15 (curve d in Figure 3). Five storms of this magnitude occurring within a 2 wk period are not likely. However, our predicted mortality rates of between 10 and 20% d^{-1} for more common wind conditions (Fig. 4) are in the same range as rates calculated from field data (see figure 1 of Peterman and Bradford 1987).

Food Limiting Conditions

The next model experimentation was conducted to determine the circumstances under which wind events might prove beneficial. Up to this point we have assumed that initial prey concentrations near the surface are sufficient to support optimal growth of northern anchovy larvae before any wind mixing disperses these concentrations. As we have seen above, under these circumstances, all wind events are detrimental to developing larvae. However, we shall now demonstrate that if initial food levels are not sufficient for rapid growth of larvae, a storm may actually enhance the survival of larvae emerging from the yolk-sac stage after the storm.

The initial condition profiles of phytoplankton, zooplankton, and nutrients for the case of insufficient, prestorm prey concentrations are shown in Figure 5a. Notice that the concentration of zooplankton near the surface is only 2.7 μg atom N ℓ^{-1} where the initial concentration of zooplankton in the previous simulations was 3.7 μg atom N ℓ^{-1}. As before, it is assumed that only 25% of this total zooplankton biomass is suitable as food for larval anchovy (estimated from data of Mullin et al. 1985). With this food limiting condition, the growth rate of northern anchovy larvae feeding near the surface is only 15% d^{-1}. The mortality rate of the larvae

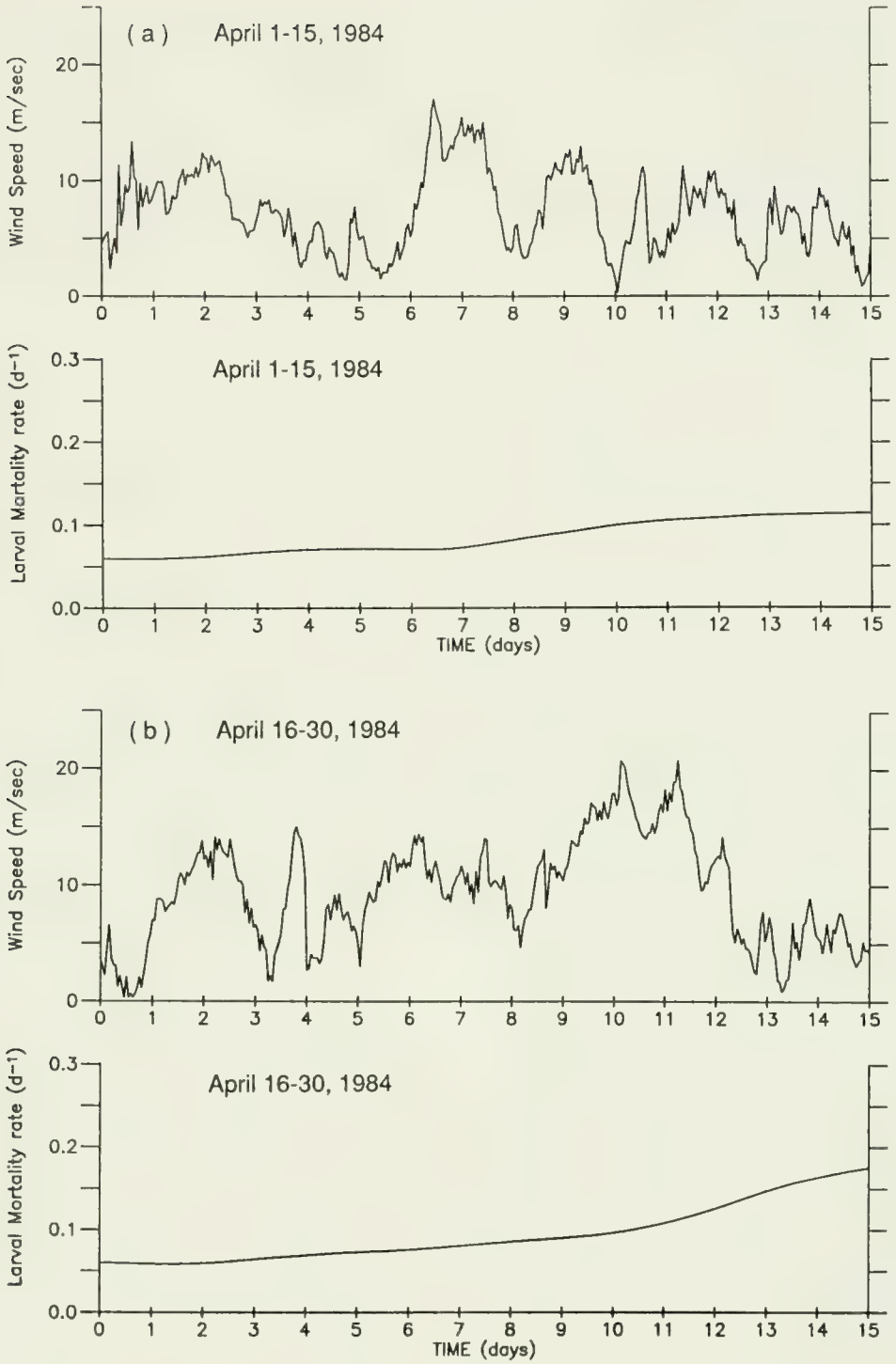

FIGURE 4.—Larva mortality rate of the northern anchovy predicted by the model using wind data from April 1984 recorded by NDBO (National Data Buoy Office, NOAA) mooring 46012 located at lat. 37.4°N, long. 122.7°W. The wind record is typical for the southern California coast in spring. (a) The wind speed and larva mortality rate for the period 1–15 April. Day zero is the day of first feeding for larvae emerging from the yolk-sac stage on 1 April. (b) Same as (a) but for the period 16–30 April, with first feeding beginning on 16 April.

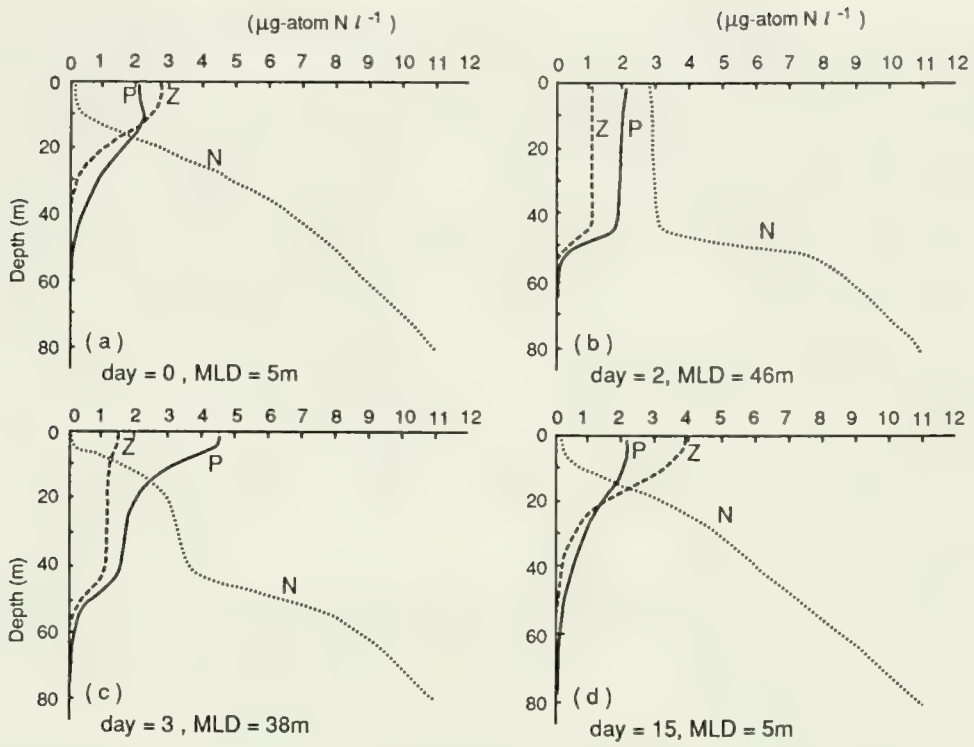

FIGURE 5.—Temporal evolution of the plankton model in response to a wind event of 20 m s^{-1} blowing for 48 hours. The initial conditions shown in (a) are different from those in Figure 1a, as the nitrate concentration continues to increase with depth. This allows more nutrients to be added to the euphotic zone by wind mixing. The initial zooplankton concentration is less than sufficient for optimal growth of northern anchovy larvae.

increases over time even in the absence of any wind event (Fig. 6, curve a).

With these initial conditions, we now determine the influence of a storm with a wind speed of 20 m s^{-1} blowing for 48 hours. The mixed layer deepens to 46 m, entraining nutrients into the euphotic zone while dissipating the existing vertical structure in the upper plankton and nutrient profiles (Fig. 5b). Curve b in Figure 6 shows the decrease in the zooplankton concentration at 3 m depth because of this mixing. However, after the winds cease and turbulence in the water column dissipates, the zooplankton concentration begins to increase. Zooplankton biomass increases as the grazers utilize increased phytoplankton biomass (Fig. 5d). By day 6 (four days after the storm) the zooplankton concentration has surpassed the initial concentration, and by day 8 it has reached concentrations high enough to support optimal growth of anchovy larvae.

However only larvae beginning to feed after the storm truly benefit from poststorm increases in zooplankton biomass. Larvae which existed before and during the storm are adversely affected by the initial decrease in prey concentrations owing to wind mixing. Their growth rate slows and their mortality rate increases to 30% per day by model day 6 (Fig. 6, curve c). But larvae entering the first-feeding stage two days after the storm when zooplankton concentrations are increasing have only a slight initial increase in mortality rate, and then a decrease (Fig. 6, curve d). Larvae emerging from the yolk-sac stage four days after the storm has passed, experience a reduction in mortality even below the initial rate of 6% per day (Fig. 6, curve e) because there is sufficient prey concentrations to support optimal growth.

DISCUSSION

It would appear advantageous for adult northern anchovy to spawn after a storm, so that by the time the eggs hatch and the larvae emerge from the yolk-sac stage, the first-feeding larvae will have high concentrations of prey (induced by the storm) upon which to feed. There is recent evidence that Atlantic menhaden, *Brevoortia tyrannus*, are stimulated to spawn by the pas-

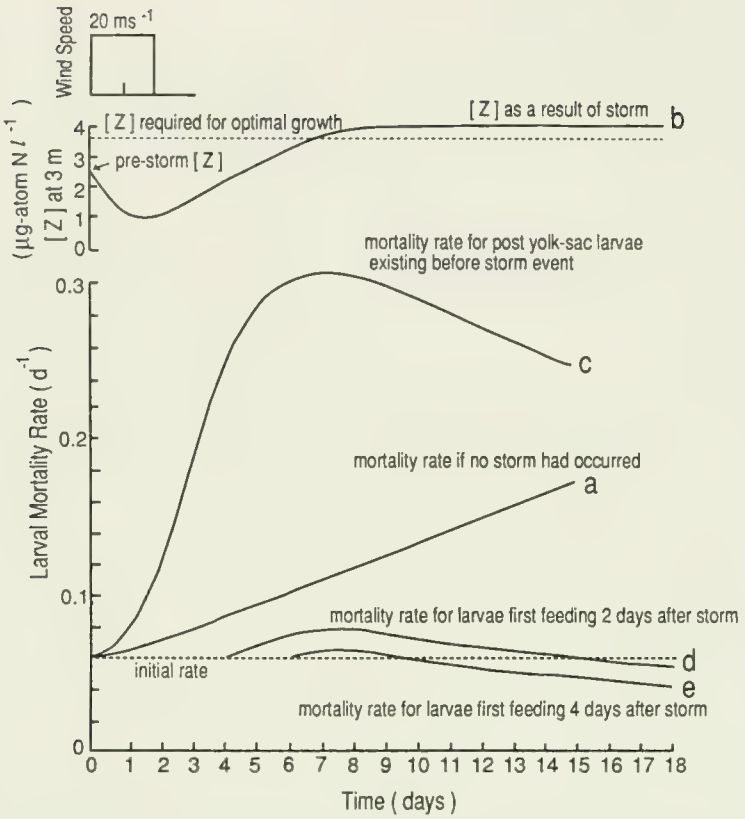

FIGURE 6.—Mortality rate predicted for larval northern anchovy positioned at 3 m depth in the simulation shown in Figure 5. Curve a shows the predicted mortality rate where winds are calm during the simulated 15 d period. Mortality rate increases because food is limiting larva growth. Curve b shows the increase in zooplankton biomass at 3 m depth owing to the wind event which entrains nutrients into the euphotic zone. Curve c shows the predicted mortality rate for larvae feeding in the water column during and after the storm. Day zero is the day of first feeding for the cohort of larvae described in curves a and c. Curves d and e show the enhanced survival of larvae first feeding 2 days and 4 days respectively, after passage of the storm.

sage of a storm (Checkley et al. 1988). The strategy of northern anchovy is to spawn continuously (Methot 1981) so that some larvae will be emerging from the yolk-sac stage at just the right time to feed upon high concentrations of microzooplankton induced by a storm.

Since any wind event which falls on the heals of the first beneficial storm will be detrimental, optimal conditions consist of a storm followed by a period of calm during which the larvae can grow into a less vulnerable stage. Any beneficial effect of the first storm will depend on the time required to concentrate new prey biomass. If the first storm is quickly followed by subsequent wind events, the prey will remain disbursed and the first-feeding larvae may not withstand the starvation period. But if the storm is followed by a period of calm winds, turbulence will dissipate, the water column will restratify, and the enhanced secondary production will become concentrated. As the time to complete development from post-yolk-sac stage to this less vulnerable stage is about 15 days (O'Connell 1980), a 2 wk period of calm following a storm strong enough to deepen the mixed layer into the nutricline is theoretically ideal for the survival of the northern anchovy larvae.

These theoretical results may apply as well to other clupeoid species, such as the Atlantic menhaden. Checkley et al. (1988) inferred that the adaptive significance of spawning by *B. tyrannus* during storms derives, in part, from the enhancement of microzooplankton prey for young larvae owing to the storm-induced upwelling. One criterion for maximal survival of the larvae of any clupeoid species would be a close

match between the interstorm duration and the critical development period of the larvae, i.e., the development to a stage where starvation is no longer a major factor.

Survival of northern anchovy larvae in the sea depends on the right type (50–100 μ in size and high nutritional quality) of prey being present in abundance at first feeding (O'Connell and Raymond 1970). Lasker (1975) maintained that the dinoflagellate *Gymnodinium splendens* is small enough to be ingested, has sufficient nutritional qualities, and is abundant enough in subsurface layers to sustain first-feeding anchovy larvae. Lasker regarded microzooplankton as not abundant enough to contribute significantly to larval survival during the first week of life.

Let us assume for the moment that *G. splendens* is the preferred prey of first-feeding anchovy larvae. Let us also assume that this dinoflagellate species is present in the phytoplankton community after a wind event (e.g., as observed by Mullin et al. 1985). The concentration of this motile organism after a wind event depends on its ability to aggregate in the face of turbulent mixing in the water column.

Wroblewski (1984) showed that the vertical diffusivity which just balances the dinoflagellates' ability to aggregate is given by

$$K_v = H W_s$$

where H is the vertical scale of the dinoflagellate layer and W_s is the swimming speed of the dinoflagellate. Cullen and Horrigan (1981) found that if nitrate is available in the upper water column (as after a strong storm), *G. splendens* will migrate to the surface into a layer several meters thick. If the wind event is weak and nitrate is not available in the surface layer, the dinoflagellates will aggregate near the nitracline in a subsurface layer. Assuming H is 5 m and W_s is 1 m h^{-1} (Kiefer and Lasker 1975; Cullen 1985), *G. splendens* should be able to aggregate against a diffusivity of 14×10^{-4} m^2 s^{-1}.

In our model, K_v quickly decays to a background diffusivity of 1×10^{-4} m^2 s^{-1} after cessation of wind forcing (Fig. 2b). Solar heating adds buoyancy at the surface and the turbulent kinetic energy in the mixed layer dissipates through friction. Thus, first-feeding northern anchovy larvae should be able to subsist on layers of *G. splendens* within a day after a storm. The short period of starvation when *G. splendens* are dispersed during the storm should not result in a significant increase in larvae mortality, unless the storm continues for several days. A few days after successful first feeding, the developing anchovy larvae must include microzooplankton in their diet. Our assumption that anchovy larvae feed on microzooplankton is appropriate when simulating larvae mortality over a 15 d period from first feeding.

The concentration of prey required for survival of anchovy larvae is controversial. The laboratory feeding experiment of O'Connell and Raymond (1970) indicated a prey concentration > 800 copepod nauplii ℓ^{-1} were required for maximal survival. More recent laboratory experiments (Houde and Schekter 1981; Munk and Kiorboe 1985) suggest the minimum concentration of prey may be as low as 200 copepod nauplii ℓ^{-1}, but of course the larvae would be expected to grow at a much slower rate (O'Connell and Raymond 1970).

Even concentrations of 200 nauplii ℓ^{-1} are high compared to estimates of *average* densities of microzooplankton in the sea (Beers and Steward 1967). However, as pointed out by Owen (1989), maximal concentration of prey rather than average concentration (estimated from integrating net hauls or pump samples) is the relevant quantity.

The highest zooplankton concentration in the model (at 3 m depth in Figure 1a) is about 4 μg atom N ℓ^{-1} of which 25% or 1 μg atom N ℓ^{-1} is larval anchovy food (e.g., copepod nauplii). This is equivalent to about 14 μg N ℓ^{-1} of copepod nauplii. The nitrogen content of *Paracalanus* stage I nauplii is about 5 ng (Checkley 1980) and of *Calanus* is about 20 ng (Corner et al. 1965; Mullin and Brooks 1967). Thus, 14 μg N ℓ^{-1} of copepod nauplii is equivalent to 2,800 *Paracalanus* stage I nauplii ℓ^{-1} or 700 *Calanus* stage I nauplii ℓ^{-1}. These concentrations correspond roughly to the prey densities used experimentally by O'Connell and Raymond 1970), but are two orders of magnitude higher than the median numbers m^{-3} observed in pump samples from the sea taken by Mullin et al. (1985) before and after a storm.

The overestimation of zooplankton biomass in the model is due to the omission of vertical loss processes such as sinking of phytoplankton and zooplankton fecal pellets which reduce the total nitrogen available to the plankton ecosystem in the upper water column (Walsh 1983; Checkley 1985). However, we would get the same response in the mortality of larval anchovy presented above, if we altered the model to simulate more realistic zooplankton concentrations, while

also reducing the concentration of prey required for the baseline growth rate of the anchovy larvae. The crux of the model is the lowering of prey concentration due to wind mixing, a corresponding decrease in ingestion and growth rate of anchovy larvae, and an increase over time of the larval mortality rate with suppressed growth.

Owen (1989) showed that microzooplankton do occur in concentrations greater than 100 organisms ℓ^{-1} on the microscale (centimeters) in patches of fine scale (meter) size. Owen found that concentrations of organisms within the patches were greater at low wind speeds. Motile organisms showed higher patch concentrations than would be expected solely from reproduction of the organisms. Rothschild and Osborne (1988) discovered mathematically that a beneficial effect of moderate turbulence is to increase the encounter rate of prey and predator on these microscales. These recent observations and theory emphasize the need to examine the feeding and survival of larval northern anchovy on microscale and fine scales. Our model with a 2.5 m vertical grid spacing does not resolve biological and physical processes on these scales. Future modeling research should compare the beneficial (e.g., productivity enhancement) and detrimental (e.g., prey dispersion) effects of storm-induced mixing on the microscale feeding environment of larval anchovy (see Vlymen 1977; Lasker and Zweifel 1978).

We conclude that wind conditions during the spawning period which are optimal for the survival of northern anchovy larvae encompass 1) wind speeds high enough (>10 m s^{-1}, depending on the water column stratification) to deepen the mixed layer into the nutricline; 2) wind event durations long enough (greater than half an inertial period, or about 8 hours at lat. 35°N) to maximally deepen the mixed layer, but short enough to maximize calm periods between storms; and 3) wind event frequency low enough (one major storm every two weeks) to allow development of larvae to a stage where carbohydrate, protein, and lipid reserves can mitigate subsequent starvation periods (about 15 days of development, depending on water column temperature).

Our conclusions are supported by the observation that northern anchovy populations off central and southern California spawn during the winter and spring months, when wind conditions can be optimal by our theoretical calculations. They do not spawn during the summer when winds are most calm and the water column is highly stratified, as one would expect considering Lasker's hypothesis alone.

ACKNOWLEDGMENTS

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Precision and Bias of Estimates of Larval Mortality

Nancy C. H. Lo, John R. Hunter, and Roger P. Hewitt

ABSTRACT: The results of four ichthyoplankton surveys conducted during January through April 1984 off the coast of California were used as the basis for Monte Carlo simulation of populations of northern anchovy, *Engraulis mordax*, larvae. The simulated populations were sampled and larval mortality rate was calculated, using established analytical procedures. Results may be used to determine the precision of an estimate of larval mortality rate and to determine the number of plankton tows required to detect a difference in mortality rates between two surveys. The estimated mortality rate was found to be biased high when the larval growth rate is overestimated and biased low when the growth rate is underestimated. The bias is asymmetrically distributed and greatest when the assumed growth substantially overestimates the real growth. The results justify interannual comparisons of larval anchovy mortality rates when interannual variation in larval growth is less than twofold. The results also indicate that the sample size required for adequate precision of estimates of mortality rates is modest compared to that required for adequate representation of the spawning season and larval habitat.

The early life stages of several fish have been extensively studied as they are the link between the present adult stock and some future recruitment to the adult stock. Frustrated with the apparent lack of a clear relationship between stock and recruitment, fishery scientists have focused attention on events during the larval stage and their ultimate effect on survival to the juvenile and adult stages. Several hypotheses have been proposed (e.g., Hjort 1913); however, an understanding of the precision and accuracy of estimates of larval mortality rates is necessary to distinguish among them (Gulland 1971). This paper draws upon our experience with the northern anchovy, *Engraulis mordax*, to address this issue.

We focus on three questions: 1) What is the minimum number of plankton tows required to estimate the mortality rate of young larvae (<20 days old) for a given coefficient of variation? 2) What is the minimum number of plankton tows required to detect a difference in the mortality rates of young larvae between two surveys? 3) How does violation of the assumption of a constant growth model affect the estimate of larval mortality?

Several biases associated with sampling northern anchovy larvae have been identified and quantified. Pelagic ichthyoplankton are caught by lowering a fine-mesh net to a depth below the larval habitat and by steadily retrieving it to the surface of the ocean (Smith and Richardson 1977). Variability in the volume of water filtered per unit of depth affects the number of larvae captured; Ahlstrom (1948) formulated the "standard haul factor" to adjust for this bias. Larvae are extruded through the meshes of the sampling gear: retention rates can be expressed as a function of larval length and mesh size (Lenarz 1972; Zweifel and Smith 1981; Lo 1983). Larvae also evade capture as evidenced by differences in the night and day catch rates (Ahlstrom 1954; Smith 1981): retention rates can be expressed as a function of larval length and the diurnal time of capture (Hewitt and Methot 1982). The apparent length of larvae is affected by abrasion from the sampling net and by the preservative solution: live larval length may be expressed as a function of preserved larval length and the duration of the plankton tow (Theilacker 1980).

The application of these corrections yields unbiased estimates of the density of larvae in each of several length categories. Age-specific variations in growth introduce variability in the duration of time that a larva of given length is vulnerable to capture. The density of larvae divided by the duration of growth through each length category yields estimates of the number of larvae of a given age produced per unit sea-surface-area per unit time, which is termed larval production (Hewitt and Methot 1982). Yolk-sac larvae growth has been described as a function of temperature (Zweifel and Lasker

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1976; Lo 1983). Growth of feeding larvae has been described as a function of season (Methot and Hewitt 1980[1]). Interannual variations in growth have not been described, and in the absence of additional information, a larval growth model with constant coefficients is used for all years. The set of coefficients encompassed temperature effects as well as seasonal effects. The rate of decline of larval production with age represents the mortality rate (Hewitt 1981).

In actual practice, a negative binomial-weighted model (Bissel 1972) has been employed to convert length-specific distributions of larval density to unbiased age-specific distributions of larval production, assuming one set of size-specific extrusion and voidance rates (Zweifel and Smith 1981; Hewitt 1982; Hewitt and Methot 1982; Hewitt and Brewer 1983; Picquelle and Hewitt 1983, 1984; Lo 1985). The negative binomial distribution is recommended for describing sample counts of fish eggs and larvae (Smith and Richardson 1977); the distribution is capable of adequately describing patchy spatial distribution patterns. The arithmetic means of these distributions describe the mortality (or production) of larvae with age.

Although the negative binomial-weighted model produces an estimate of the variance of the mean density at a particular age, each age-specific distribution is unique because of the spatial dispersal of the larvae (Hewitt 1981). The variance of the mean density is underestimated as the extrusion and avoidance are assumed to be constant, and the variance about the mortality curve (hence, the variance of the mortality rate) is not easily determined. In the simulation, random variation of avoidance of the net and extrusion through the meshes of the net were included so that the variance of the mortality rate might best be evaluated. The approach used here is to construct a simulated population, sample it with simulated surveys, and estimate the mortality rate of larvae, using the procedures described above. By conducting many surveys, the accuracy and precision of the estimates of mortality rates may be investigated.

Potential biases in estimating larval mortality, introduced by assuming no interannual variation in growth, were our main concern and were investigated by simulation. Growth rates were varied when constructing the populations; mortality rates were subsequently calculated assuming a set of growth rates (i.e., no interannual variation). By comparing the calculated mortality rates to a known rate, the magnitude of biases may be investigated.

METHODS

A Monte Carlo simulation model (Fig. 1) was employed to address the questions pertaining to the biases and precision of the estimate of larval mortality. A population of anchovy larvae was constructed using observed seasonal and geographic distributions. A known mortality rate was imposed on the population and sampling effort was varied over time and space. Known sampling biases were imposed and then adjusted for using the same techniques for calculating larval mortality rate as have been used on real surveys. Several hundred simulated surveys were conducted to assess the accuracy and precision of the estimates of mortality rates. Simulated larval growth was also varied to determine the sensitivity of the estimates of mortality rates to an assumption of constant larval growth. The details of this simulation are outlined in the following paragraphs.

Larval Population

A series of CalCOFI[2] ichthyoplankton cruises conducted in 1984 (Fig. 2) was used as a basis for constructing the population of larvae in the ocean. The total abundance of anchovy larvae at each station was adjusted for extrusion of small larvae through the meshes of the net (Fig. 3) and avoidance of the net by large larvae (Fig. 4). The adjusted catches were then stratified by geographic region (Fig. 2), month, and temperature. The negative binomial distribution was fit to the observations (positive tows only) in each region-month-temperature cell owing to the patchiness of larvae and the fact that the mean larval abundance is less than the standard deviation in general (Table 1). Samples were randomly drawn from these distributions (where the variate was the total number of larvae <9.25 mm per station) to conduct a simulated survey.

[1]Methot, R. D., Jr., and R. P. Hewitt. 1980. A generalized growth curve for young anchovy larvae: derivation and tabular example. SWFC Admin. Rep. LJ-80-17, 8 p.

[2]California Cooperative Oceanic Fisheries Investigations (CalCOFI) is a consortium of marine institutions engaged in long-term monitoring and study of the pelagic ecology of the California Current. Large-scale ichthyoplankton surveys have been conducted since 1949. See Hewitt 1988, Reid 1988, and Smith and Moser 1988 for reviews.

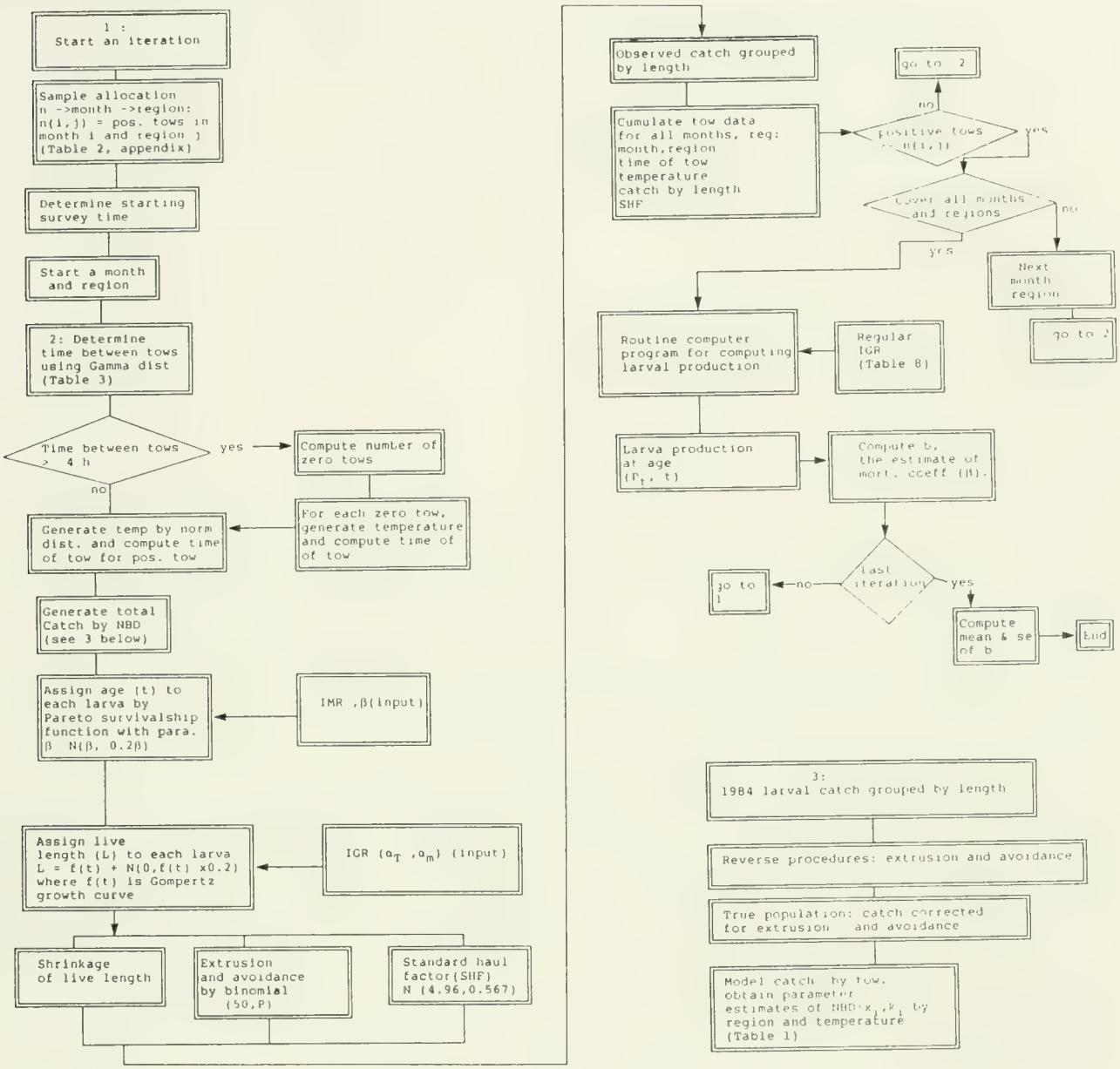


FIGURE 1.—Flow chart of the simulation.

Allocation of Sampling Effort

Simulated population encountered by plankton tows was computed according to their distribution in 1984 by month and region (Table 1). The portion of simulated tows that contained anchovy larvae was similarly determined (Table 2; App.). In this way, the sample size (number of tows) could be varied and yet still retain the spatial and temporal distribution of sampling effort that was used in 1984. The time of the simulated tows was assigned by randomly selecting a value from a Gamma distribution fitted to the actual time between tows in each region (Table 3; App.).

Larval Mortality Rate

Because it was found that anchovy larvae suffer higher mortality during the first-feeding period than during later stages, a Pareto function describes the survival of anchovy larvae younger than 20 days adequately (Hewitt and Brewer 1983; Lo 1985, 1986). In the present study, we used the Pareto function to assign age to the larvae in the population (Table 1; Fig. 5; App.).

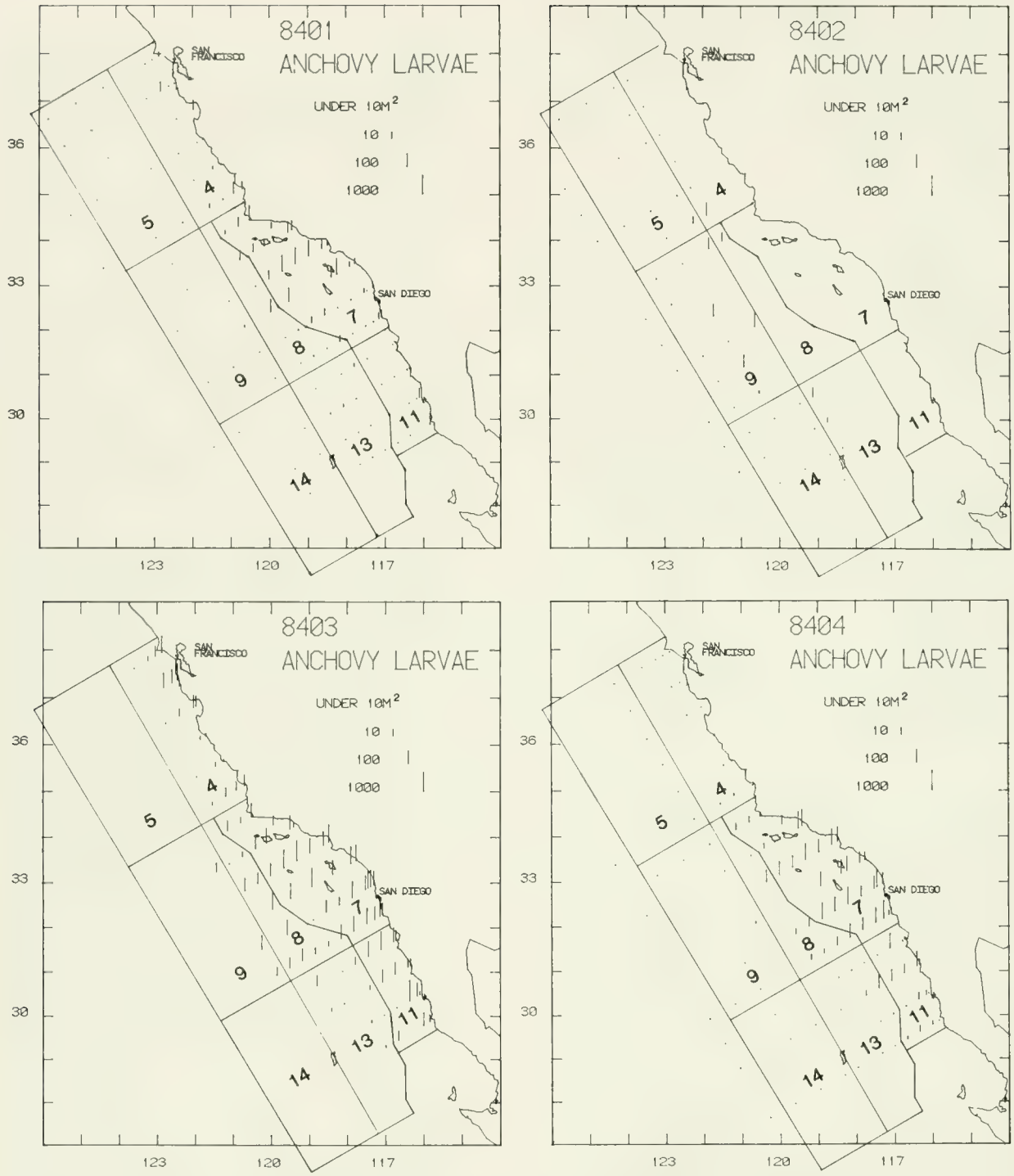


FIGURE 2.—Description of the seasonal and geographic distribution of sampling effort on a series of ichthyoplankton cruises conducted off the coast of California in 1984. The abundance of anchovy larvae at each station is indicated by the height of the "tree." Stations are grouped into geographic regions 4 through 14.

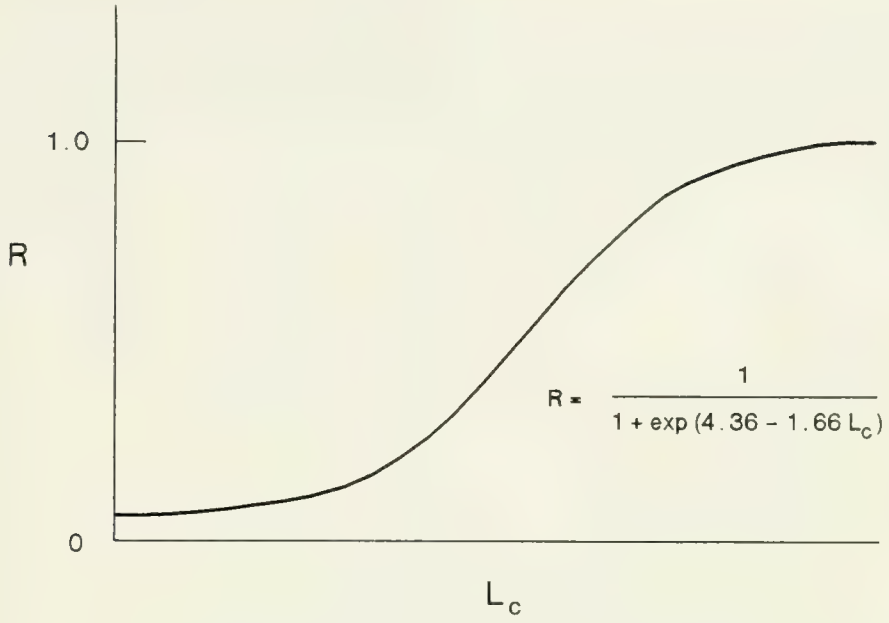
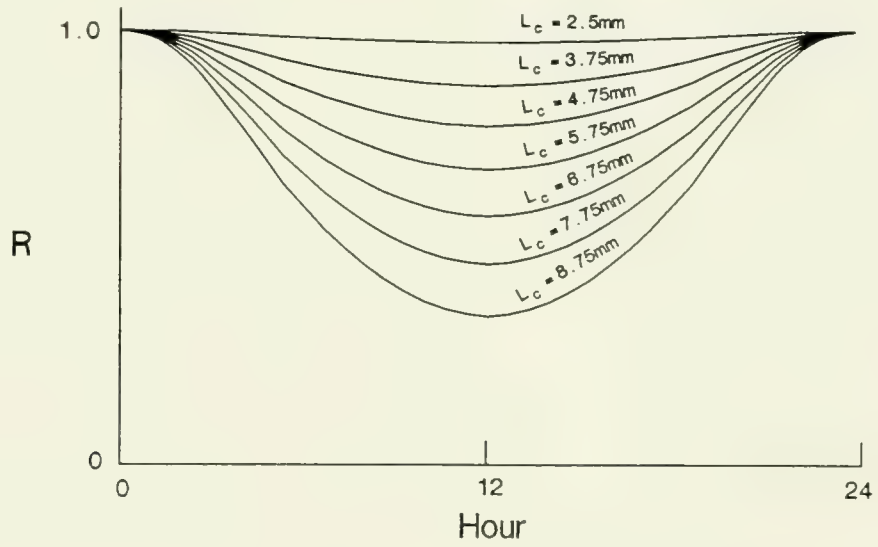


FIGURE 3.—Retention of anchovy larvae not extruded through the meshes of a plankton net constructed of 0.505 mm nylon (Lo 1983). R is the portion of larvae, of preserved length L_c, retained in the net.



$$R = \left(\frac{1 + DN_L}{2}\right) + \left(\frac{1 - DN_L}{2}\right) \cos\left(\frac{2\pi \star Hour}{24}\right)$$

where:

L_c	DN_L
2.5	1.67
3.75	1.47
4.75	1.46
5.75	1.27
6.75	1.21
7.75	1.16
8.75	1.13

FIGURE 4.—Retention of anchovy larvae which have not avoided capture (Hewitt and Methot 1982). R is the portion of larvae, of preserved length L_c, retained in the net. DN_L is the length-specific day/night catch ratio.

TABLE 1.—Simulated population of anchovy larvae based on a series of ichthyoplankton surveys conducted in 1984. Tabulated values are the parameters (m and k) of negative binomial distributions[1] fit to the population stratified by month, region, and temperature.

		Temperature °C							
		≤13°		13.1°–14°		14.1°–15°		>15°	
Month	Region	m	k	m	k	m	k	m	k
1	4	31.25	0.39	63.00	0.34	27.50	0.51	27.50	0.51
	5	[2]0.25	∝	0.25	∝	0.25	∝	0.25	∝
	7	270.50	0.62	270.50	0.62	147.08	0.25	619.10	0.14
	8	2.00	∝	2.00	0.31	44.00	0.22	98.60	0.22
	9	34.00	0.60	34.00	0.60	136.00	0.41	51.00	4.33
	11	56.80	0.55	56.80	0.55	56.80	0.55	56.80	0.55
	13	6.80	0.37	6.80	0.37	6.80	0.37	6.80	0.37
	14	0.25	∝	0.25	∝	0.25	∝	0.25	∝
2	4	558.17	0.64	120.50	0.32	22.50	0.97	22.50	0.97
	5	0.25	∝	0.25	∝	0.25	∝	0.25	∝
	7	270.50	0.62	270.50	0.62	147.08	0.25	619.10	0.14
	8	2.00	∝	2.00	0.31	44.00	0.22	98.60	0.22
	9	34.00	0.60	34.00	0.60	136.00	0.41	51.00	4.33
	11	56.80	0.55	56.80	0.55	56.80	0.55	56.80	0.55
	13	6.80	0.37	6.80	0.37	6.80	0.37	6.80	0.37
	14	0.25	∝	0.25	∝	0.25	∝	0.25	∝
3	4	2.00	0.40	2.00	0.40	2.00	0.40	2.00	0.40
	5	0.25	∝	0.25	∝	0.25	∝	0.25	∝
	7	4.00	5.39	7.33	5.39	522.33	1.07	790.60	1.38
	8	117.50	0.50	117.50	0.50	520.00	0.20	206.30	0.45
	9	0.00	0.00	0.00	0.00	150.50	0.78	150.50	0.78
	11	14.50	2.14	14.50	2.14	147.00	1.22	514.30	0.45
	13	6.80	0.37	6.80	0.37	6.80	0.37	6.80	0.37
	14	0.25	∝	0.25	∝	0.25	∝	0.25	∝
	4	2.00	0.40	2.00	0.40	2.00	0.40	2.00	0.40
	5	0.25	∝	0.25	∝	0.25	∝	0.25	∝
	7	4.00	5.39	7.33	5.39	522.33	1.07	790.60	1.38
	8	117.50	0.50	117.50	0.50	520.00	0.20	206.30	0.45
	9	0.00	0.00	0.00	0.00	150.50	0.78	150.50	0.78
	11	14.50	2.14	14.50	2.14	147.00	1.22	514.30	0.45
	13	6.80	0.37	6.80	0.37	6.80	0.37	6.80	0.37
	14	0.25	∝	0.25	∝	0.25	∝	0.25	∝

[1]Negative binomial distribution where

$$P(X - x) = \frac{(x + k - 1)!}{x!(k - 1)!} * [m/m + k)]^x * [k/m + k)]^k \text{ for } x = 0,1,2,3,....$$

[2]Poisson distribution was used where $P(X = x) = (m^x e^{-m})/x!$ for $x = 0,1,2,3,.$.

A two-step Gompertz growth curve (Fig. 6) was used to determine the corresponding larval length. The length at age was generated based on a normal distribution with mean equal to the length computed from the Gompertz growth curve and a standard deviation equal to 0.2 times the length. (The standard deviation is normally proportional to the mean length at age.) The coefficient of variation of 0.2 was arbitrarily chosen because no direct estimate of the standard deviation was available. These simulated larvae, with assigned ages and lengths, composed the catches.

Sampling Biases

The simulated catches were reduced to account for the effects of extrusion and avoidance.

TABLE 2.—Distribution of sampling effort during January through April 1984 by region and month, where $p(i)$ is the *proportion of tows for month i* and $\Sigma p(i) = 1$, $g(j|i)$ is the proportion of tows made in region j during month i and $\Sigma q(j|i) = 1$, and $r(j|i)$ is the proportion of positive tows for region j during month i and $0 \leq f(j|i) \leq 1$. The number of tows is indicated by N, and the positive tows are indicated by n (i.e., those tows which contained anchovy larvae)

	January		February		March		April		Total
i =	1		2		3		4		
N =	139		89		67		54		349
n =	55		55		47		19		176
$p(i)$	0.40		0.26		0.19		0.15		0.50
Region	q	r	q	r	q	r	q	r	
4	0.14	0.43	0.28	0.29	0	—	0.36	0.14	
5	0.14	0.06	0.20	0.06	0	—	0.15	0	
7	0.25	0.90	0.21	1.00	0.26	0.94	0.26	0.93	
8	0.04	0.67	0.01	1.00	0.14	0.88	0.02	1.00	
9	0.13	0.06	0.16	0.63	0.02	1.00	0.16	0.11	
11	0.14	0.33	0.06	0	0.24	0.88	0.05	0	
13	0.09	0.27	0.02	1.00	0.25	0.41	0	—	
14	0.07	0.08	0.06	0.17	0.09	0	0	—	
	1.00		1.00		1.00		1.00		

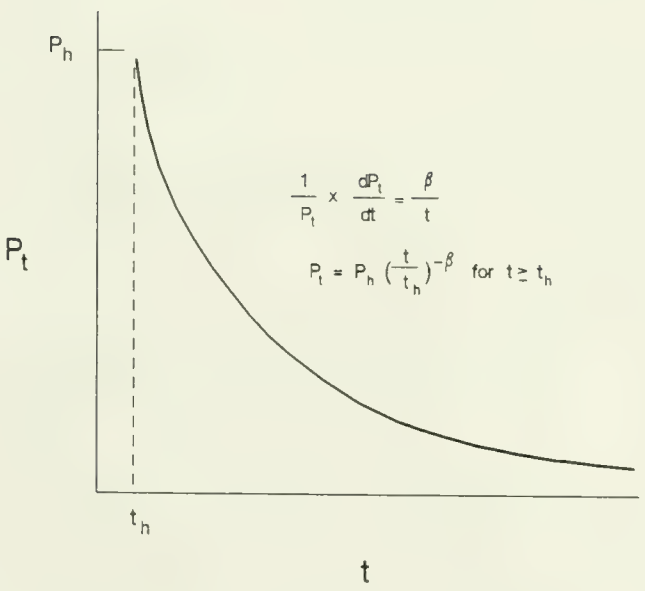


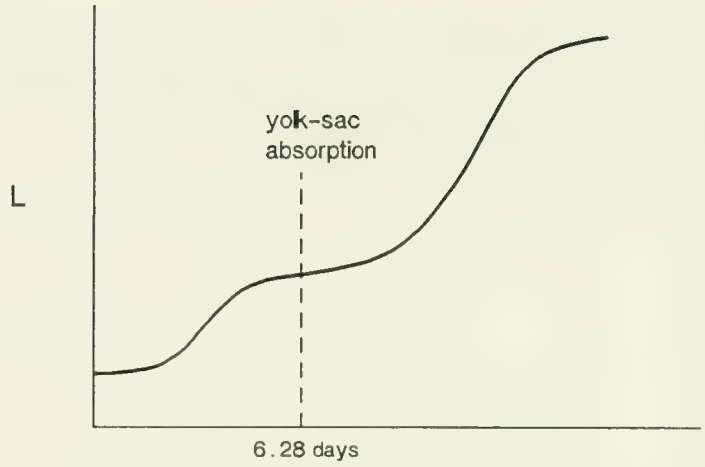
FIGURE 5.—Pareto model of larval production where larval mortality is assumed to decline with increasing age (Lo 1985 and 1986). P_t is the daily production of larvae at age t; β is the mortality coefficient; and t_h is the age at hatch.

TABLE 3.—Two parameters describing Gamma distributions[1] fit to the time between tows minus the constant in each region. Each of these distributions is shifted by the addition of the constant listed. The constant is the minimum time (hours) between two positive tows.

Regional	α	β	Constant
4	0.275	43.71	2
5	0.510	3.92	4
7	0.291	34.93	2
8	0.346	42.19	3
9	0.838	39.47	4
11	0.714	5.03	2
13	0.561	21.08	3
14	0.500	69.00	4

[1]Gamma distribution where

$$g(x) = \frac{1}{\beta(\alpha - 1)!} (x/\beta)^{(\alpha-1)} \exp(-x/\beta) \text{ for } x > 0$$



$$L = 4.25 \left(\frac{0.32}{4.25}\right)^{e^{-\alpha_T t}} \text{ for } t \leq 6.28 \text{ days}$$

$$L = 27 \left(\frac{4.1}{27}\right)^{e^{-\alpha_m t}} \text{ for } t > 6.28 \text{ days}$$

Where: $\alpha_T = a_T \exp(b_T \times \text{TEMPERATURE})$

$= 0.11 \exp(0.12 \times \text{TEMPERATURE})$

$\alpha_m = (a_m - b_m \times \text{MONTH})^{-1}$

$= (22.48 - 0.83 \times \text{MONTH})^{-1}$

FIGURE 6.—Temperature-dependent and season-dependent larval growth curves (Methot and Hewitt 1980; Lo 1983). Gompertz models are used to describe each growth phase where α_T is the temperature-dependent growth coefficient and α_m is the season-dependent growth coefficient.

The fraction, p, of larvae extruded through the mesh or avoiding the net was generated by a sample mean of a binomial random variable, y, with parameters N and P. The parameter: N was set to 50 and P was the length-specific extrusion rate or avoidance rate from the same equations used to construct the population from the 1984 surveys. Thus p equaled $y/50$. Although p has a mean of P, it was not necessarily equal to P for each simulation run. The live lengths of larvae were reduced to account for the effects of net abrasion and preservaton effects (Theilacker 1980; Fig. 7). A standard haul factor was selected from the observed normal distribution of this variate (mean = 4.96, SD = 0.567) and used to index the volume of water filtered per unit of depth sampled. These catches then formed the raw material for the mortality estimation procedure.

Estimating Mortality Rate

The larvae in each catch were grouped into 1 mm length categories. A weighted negative binomial distribution was fitted to each length category where the original variate was the number of larvae (of a given length category) per station. Using this procedure, each observation was weighted for the effects of sampling biases (extrusion, avoidance, volume of water filtered, growth and shrinkage). The final variate was the number of larvae (of a given age) produced per day per 0.05 m^2 of sea surface. The rate at which larval production declines with time was defined as the mortality rate. For the Pareto model, the mortality rate was assumed to decline with age and mortality was indexed by the mortality coefficient (β). For the simulations described in this report, β was estimated as the slope of the log-

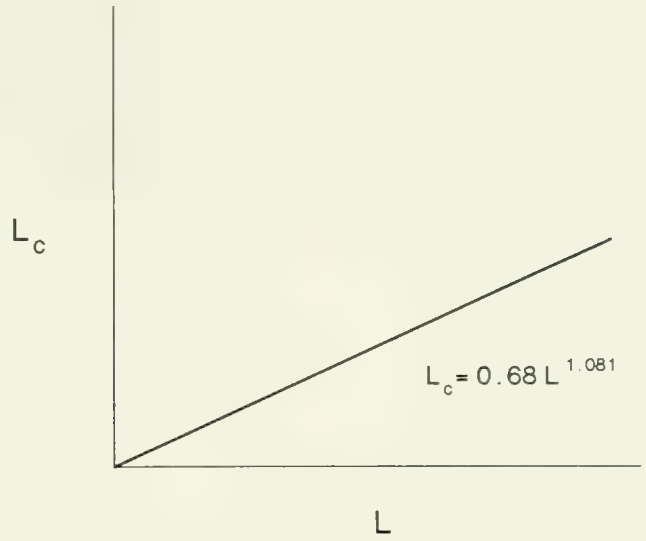


FIGURE 7.—The effect of net abrasion and preservative on the apparent length of anchovy larvae (from Theilacker 1980). L is live larval length; L_c is preserved (captured) larval length, and the length of the plankton tow is 20 minutes.

transformed Pareto function:

$$\ln(P_t) = \ln(P_h) - \beta \ln(t/t_h) .$$

Each simulation that produced an estimate of mortality rate was repeated many times. The collection of estimates of mortality rates was used to assess the accuracy and precision of estimates of mortality rates.

Sample Size for Detecting a Difference of Mortality Rates

The minimum sample size required to detect a difference between two mortalities was computed by two methods.

The *CV* Method

The coefficient of variation (cv) of the estimate of the difference between two mortality coefficients ($D = \beta_2 - \beta_1$) was calculated by

$$cv(d) = \frac{[\text{var}(b_1) + \text{var}(b_2)]^{0.5}}{D} \quad \text{for } D \neq 0 \qquad (1)$$

where d is the estimate of D, the difference between mortality coefficients β_1 and $\beta_2 (D = \beta_2 - \beta_1)$; b_1 and b_2 are the estimates of β_1 and β_2; $\text{var}(b_1)$ and $\text{var}(b_2)$ varying with sample size are computed in the simulation. The relationship between the sample size (n) and two elements, $cv(d)$ and D, enables us to determine the minimum sample size for a given $cv(d)$ and D.

The Power Method

The probability of detecting a difference in two mortality rates, given that there is a difference, was calculated as

$$P[d > c(\beta_1,n) \mid D] = P[Z > z(\beta_1,\beta_2,n)] \qquad (2)$$

where d follows a normal distribution with a mean of D and a variance of $[\text{SE}(d)]^2$; Z follows a normal distribution with a mean of 0 and a variance of 1:

$$c(\beta_1,n) = 2\,\text{SE}(d) = 2\sqrt{2}\,\text{SE}(b) \quad \text{for } \beta_1 = \beta_2 (D = 0) \qquad (3)$$

$$z(\beta_1,\beta_2,n) = \frac{c(\beta_1,n) - D}{\text{SE}(d)}$$

$$\text{and } \text{SE}(d) = [\text{var}(b_1) + \text{var}(b_2)]^{0.5} \quad \text{for } \beta_2 \neq \beta_1 (D \neq 0).$$

A normal distribution table was used to obtain the probability values.

Relationship Between Growth and Mortality

The mortality coefficient (β) was fixed. Five

populations were constructed with data from a single region-month stratum using five combinations of growth coefficients for yolk-sac (α_T, a temperature-specific coefficient) and feeding larvae (α_m, a season-specific coefficient) (see Table 8). Each population was sampled repeatedly and an average mortality coefficient calculated assuming standard growth coefficients. These mortality coefficients were then compared with the fixed mortality coefficient used to construct the populations.

RESULTS

The simulation model was used to estimate the following: 1) the mortality coefficients and their standard errors for various sample sizes when the true mortality coefficient was fixed, 2) the difference between two mortality coefficients and its standard error for various sample sizes, and 3) the mortality coefficients, assuming various growth rates.

Estimates of β with Various Sample Sizes

The mortality coefficient (β) was fixed at 1.5 for the inshore area (regions 4, 7, 8, 11, and 13; Fig. 2) and at 0.05 for the offshore area (regions 5, 9, and 14). The lower coefficient was required to generate simulated catch curves similar to those observed in offshore areas. The low mortality coefficient observed in offshore areas was likely the result of transport of older larvae from inshore to offshore regions (Power 1986). The average mortality coefficient (β), weighted by area of each region, was 1.41.

For each sample size (50, 100, 200, 300, and 400 plankton tows) 100 computer runs were made, and an estimate of the mortality coefficient (b) was calculated. The mean mortality coefficient, its standard error, and the coefficient of variation (cv) are listed in Table 4 for each sample size. The mean mortality coefficient for all sample sizes, except 50, slightly overestimated the true value of $\beta = 1.41$. The cv decreased with increasing sample size.

The relationship between cv and the number of positive tows (n) was quantified by assuming that half of the tows contained anchovy larvae (the actual portion of positive tows in 1984 was 0.5) (Table 2).The curve (Fig. 8) may be described by the power function:

$$cv(b) = 0.418\, n^{-0.47}$$

From Figure 8 and the above expression, cv may be expected to be 0.10, 0.06, or 0.05 for 20, 60, or 100 positive tows. For $n > 100$, cv may be expected to decrease at a slow rate. Thus a survey of 120 tows, yielding 60 positive tows, is sufficient to estimate the mortality coefficient with an expected $cv = 0.06$. Data from annual surveys conducted between 1980 and 1987, where the portion of positive tows ranged from 0.47 to 0.98, are also shown on Figure 8. The variation of b, as related to sample size during 1980–87, follows the relationship estimated from a single year's data and implies that the relationship can be used as a guide for sample size determination.

TABLE 4.—Mean, standard error (SE), and coefficient of variation (cv) of estimates of the mortality coefficient (b) for various sample sizes (N), with 50% positive for anchovy larvae (n = 0.5 N), from 100 computer runs of each simulated survey.

N	n	mean	SE	cv = SE/mean
50	25	1.39	0.13	0.09
100	50	1.43	0.09	0.06
200	100	1.44	0.06	0.04
300	150	1.44	0.06	0.05
400	200	1.43	0.05	0.03

Estimates of *D* with Various Sample Sizes

The mortality coefficient (β) was fixed at 1.0, 1.5, 2.0, 2.5, and 3.0 for the inshore area (regions 4, 7, 8, 11, and 13). The inshore area was relatively well sampled and contained relatively high abundances of larvae; the proportion of positive stations in these regions was approximately 0.6 (Tables 1, 2). Estimated mortality coefficients (b) were determined for five simulated populations (corresponding to each of the five mortality coefficients (β)) using sample sizes of 50, 100, and 200 plankton tows with 60% of them positive for anchovy larvae.

The average estimated mortality coefficient and its standard error were determined after 100 computer runs and listed in Table 5. As expected, standard errors decreased with increased sample size. The estimated mortality coefficient was biased slightly low for $\beta < 2$ and biased slightly high for $\beta > 2$. The biases are negligible although they appeared to increase in magnitude as β departed from 2. The estimates of mortality rates and their standard errors were used to determine minimum sample size by two methods.

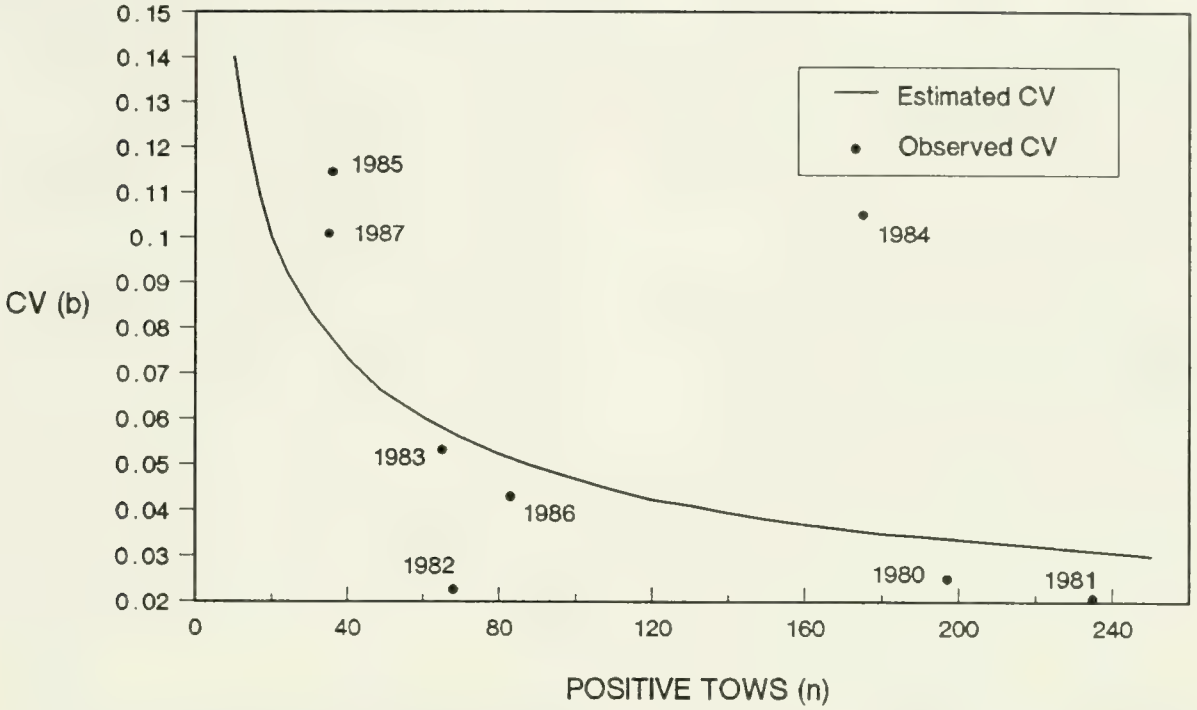


FIGURE 8.—The relationship between the coefficient of variation, cv(b), and the number of positive tows, n, derived from the results of the simulation. 1980–87 survey results are also plotted.

The *CV* Method

The cv of the estimate of the difference between two mortality coefficients, $cv(d)$ (Equation (1)), was calculated for various mortality differences and sample sizes using the data listed in Table 5. The $cv(d)$ decreases linearly with the difference between mortality coefficients (D), increases linearly with the absolute value of the larger of the two mortality coefficients (β_2), and exponentially declines with increasing sample size (N, n) (Table 6). The required sample size was thus estimated by regressing the number of positive tows on β_2, D, and $\ln[cv(d)]$:

$$n = -101 + 24.8\,\beta_2 - 150\,D - 128\,\ln[cv(d)]\,.$$

For example, estimating the difference between two estimated mortality coefficients, when the true mortality coefficients are 3.0 and

TABLE 5.—Mean and standard error (SE) of estimated mortality coefficient based on 100 computer runs. Five populations were simulated, each with a different mortality coefficient (β). Simulated surveys used three sample sizes (N) with 60% of the plankton tows positive for anchovy larvae (n).

β	Sample size $N(n)$					
	50(30)		100(60)		200(120)	
	mean	SE	mean	SE	mean	SE
1.00	0.90	0.100	0.91	0.075	0.93	0.058
1.50	1.44	0.090	1.44	0.064	1.44	0.060
2.00	1.98	0.120	1.99	0.087	2.01	0.058
2.50	2.56	0.110	2.57	0.097	2.58	0.065
3.00	3.18	0.170	3.18	0.100	3.18	0.075

TABLE 6.—Coefficient of variation of the estimate of the difference between two mortality coefficients, $cv(d)$, calculated for various mortality differences, D, and sample sizes, n. The number of positive tows, n, was 60% of the total number of tows.

$\beta_2 - \beta_1$	Sample size $N(n)$		
	50(30)	100(60)	200(120)
$D = 0.5$			
1.5 – 1.0	0.268	0.196	0.166
2.0 – 1.5	0.300	0.210	0.166
2.5 – 2.0	0.320	0.260	0.170
3.0 – 2.5	0.400	0.270	0.190
$D = 1.0$			
2.0 – 1.0	0.156	0.115	0.082
2.5 – 1.5	0.142	0.116	0.088
3.0 – 2.0	0.208	0.133	0.095
$D = 1.5$			
2.5 – 1.0	0.100	0.082	0.058
3.0 – 1.5	0.130	0.079	0.064

2.0 ($\beta_1 = 2.0$, $\beta_2 = 3.0$, $D = 1.0$), with a $cv(d) = 0.15$, will require $n = 67$ positive tows from each population. With 70 positive tows from each population, approximately 95% of the sample differences can be expected to be between 0.70 and 1.30 ($1.0 \pm 2 * 0.15$).

The Power Method

The standard error of the estimated mortality coefficient, SE(b), was modeled as a function of the number of positive tows, n, and the true mortality coefficient (β) using the data listed in Table 5:

$$SE(b) = 0.356\, n^{-0.469}\, e^{0.239\beta}.$$

The probabilities of detecting a difference between two mortality coefficients, given that there is a difference (this is referred to as the power of the test), were calculated for various sample sizes and listed in Table 7. The power increases as the difference of mortality coefficients increases, and it is equal to the level of

TABLE 7.—Probability of detecting a difference between two mortality coefficients, given one of the mortality coefficients (β_1), the true difference ($D = \beta_2 - \beta_1$), and the number of positive tows (n). Because of symmetry about $D = 0$, partial figures are listed.

	True difference (D)							
n	−2.0	−1.5	−1.0	−0.5	0.5	1.0	1.5	2.0
$\beta_1 = 1.0$								
10					0.62	0.96	1.00	1.00
20					0.86	1.00	1.00	1.00
30					0.96	1.00	1.00	1.00
40					1.00	1.00	1.00	1.00
$\beta_1 = 1.5$								
10				0.50	0.50	0.97	1.00	
20				0.79	0.75	1.00	1.00	
30				0.93	0.90	1.00	1.00	
40				0.98	0.96	1.00	1.00	
50				1.00	0.99	1.00	1.00	
60				1.00	1.00	1.00	1.00	
$\beta_1 = 2.0$								
10			0.96	0.40	0.43	0.92		
20			1.00	0.70	0.70	1.00		
30			1.00	0.86	0.86	1.00		
40			1.00	0.93	0.92	1.00		
50			1.00	0.98	0.96	1.00		
60			1.00	1.00	1.00	1.00		
$\beta_1 = 2.5$								
10		1.00	0.91	0.34	0.48			
20		1.00	0.99	0.59	0.58			
30		1.00	1.00	0.76	0.75			
40		1.00	1.00	0.86	0.86			
50		1.00	1.00	0.93	0.91			
60		1.00	1.00	0.96	0.95			
70		1.00	1.00	1.00	1.00			
$\beta_1 = 3.0$								
10	1.00	0.99	0.82	0.27				
20	1.00	1.00	0.98	0.50				
30	1.00	1.00	1.00	0.66				
40	1.00	1.00	1.00	0.78				
50	1.00	1.00	1.00	0.86				
60	1.00	1.00	1.00	0.91				
70	1.00	1.00	1.00	0.95				
80	1.00	1.00	1.00	0.97				
90	1.00	1.00	1.00	1.00				

significance ($\alpha = 0.05$) when the difference is zero. The power is symmetrical about $D = 0$; thus, only partial figures were given in Table 7.

For example, if the true difference was 0.5 and one of the mortality coefficients was 2.0, with a probability of 0.86, a sample size of 30 positive tows from each of two populations will detect a significant difference in their mortality coefficients. The probability would be only 0.76 if one of the mortality coefficients was 2.5. In general, to achieve the same probability of detecting a given difference between mortality coefficients, a larger sample size is required for a larger β. To detect a significant difference with a probability of 0.96, when the true difference is 0.5 and one of the mortality coefficients is 1.0, 30 positive tows are required from each population. If $\beta = 2.5$, however, 60 positive tows are required to detect the same difference with a probability of 0.95. If the difference is greater than 1, at most 20 positive tows from each population would be sufficient.

The two methods serve different purposes. The *cv* method provides a 95% confidence interval for the difference. The Power Method assigns a probability to the detection of a difference, but provides no information on the magnitude of the difference.

Estimates of β with Various Growth Rates

Mortality is defined as the decline of production with larval age. Thus an overestimate of larval age, predicted from an underestimate of growth rate, will underestimate mortality rate. Similarly, an overestimate of growth rate will result in an overestimate of mortality rate.

The mortality coefficient (β) was fixed at 1.5. Data from February, region 7, temperature 15°C, were used to construct five populations, corresponding to five combinations of growth coefficients for yolk-sac and feeding larvae (Table 8). Each population was surveyed 50 times with a sample size of 50 plankton tows. The estimated mortality coefficient (b) was calculated by assuming standard growth coefficients for February, region 7, temperature 15°C (Table 8). When the population growth coefficients (α_m) were underestimated by the standard coefficients, the estimated mortality coefficient (b) was less than $\beta = 1.5$; conversely when growth was overestimated, the mortality coefficient was also overestimated.

Because the yolk-sac stage is short, relative to the feeding stage, we can reasonably assume that the growth coefficient for feeding larvae (α_m) has the largest effect on the estimated mortality coefficient (b). When the estimated mortality coefficient is plotted against α_m (Fig. 9), it is apparent that the bias in estimating mortality rate, caused by errors in the assumed growth rate, is asymmetrical: greater when actual growth is slower than assumed growth and smaller when actual growth is faster than assumed. When the actual growth was half the assumed rate, the mortality coefficient was overestimated by 80%; when the actual growth was double the assumed rate, the mortality coefficient was underestimated by only 16% (Table 8).

The coefficient, α_m, determines the instantaneous growth rate (IGR) at age t as the IGR = $\alpha_m \ln(L_\infty/L_0) \exp[-\alpha_m(t - t_0)]$ where L_∞ is the maximum fish length, and L_0 is the minimum fish length for $t > 6.28$ days (Fig. 6). Large value of α_m implies that the IGR is large for the small value of age t, and the IGR decreases rapidly as the fish ages. Because both the IGR and the instantaneous mortality rate (IMR = β/t) are two different nonlinear functions of age (t), the relationship between these two coefficients (α_m and β) is also nonlinear and thus the bias is asymmetric.

TABLE 8.—Five sets of coefficients for two-step Gompertz growth curves (Fig. 6) used to simulate five populations. Also listed are the standard coefficients used in the analysis of survey data for region 7 in February with a temperature of 15°C. The estimated mortality coefficient (b) is listed as average of 50 computer runs. The true mortality coefficient (β) was 1.5.

a_T	b_T	α_T	a_m	b_m	α_m	b
0.11	0.06	0.27	44.96	0.83	0.023	2.70
0.11	0.24	4.05	11.24	0.83	0.104	1.26
0.22	0.12	1.33	22.48	0.42	0.046	1.41
0.11	0.09	0.42	33.72	0.83	0.031	1.90
0.22	0.12	1.33	16.86	0.83	0.066	1.31
Standard coefficients:						
0.11	0.12	0.67	22.48	0.83	0.048	

DISCUSSION AND CONCLUSIONS

The simulation model and its methodology have general applicability to larval fish of many species, although these results apply directly to estimates of northern anchovy larval mortality rates derived from CalCOFI surveys. Results may differ because of differences in the param-

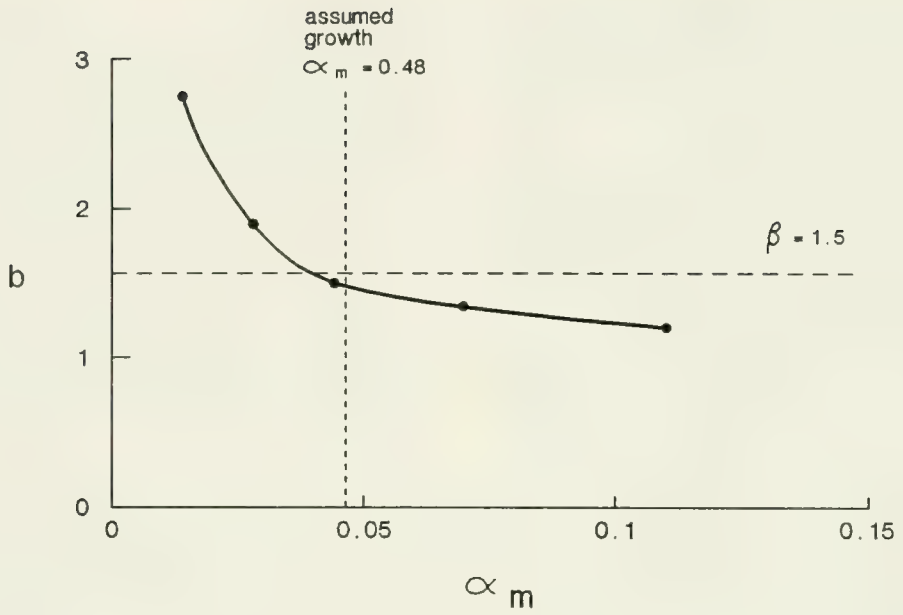


FIGURE 9.—The estimated mortality coefficient (b) is biased by errors in the assumed growth coefficient for feeding larvae, $\alpha_m = 0.48$. The true mortality coefficient (β) was 1.5.

eter values and their variances. Nevertheless, most ichthyoplankton sampling problems are sufficiently similar so that the results derived for anchovy provide a general idea of the sample size required for adequate precision of larval mortality estimates. (When using the regressions derived in this study to estimate sample size, parameter values should be within the range used in the simulation [$1.0 \leq \beta \leq 3.0$, $0.5 \leq D \leq 2.0$]. Values outside these ranges could lead to unreliable estimates of sample size.) The results also provide an assessment of the effect of biased growth rates on estimates of larval mortality rate, which has general applicability to many species.

Caveats

Application to Site-Intensive Studies

Small-scale site-intensive studies may be conducted to study underlying mechanisms of larval mortality rate by measuring larval condition, growth, starvation rates, and mortality rate in small segments of the habitat. Such studies have greater problems with bias and precision than the CalCOFI surveys where the entire spawning habitat is sampled. As noted above, an important potential bias is the transport of larvae in or out of the study area. Taggart and Leggett (1987) noted that failure to account for advective losses of larvae from a small bay resulted in a significant overestimate of mortality.

Another problem arises from the choice of study areas. Many specimens must be collected over a short period to assess growth, starvation, and other condition factors. If sites are selected that contain larval densities that are high, relative to the average density for the entire habitat, and patchy, the effect will be to increase the variance, because the variance is often positively correlated with the density of larvae (Smith and Richardson 1977), and thereby reduce the power to detect differences in mortality rate between sites. The simulations were based on large regions of anchovy habitat and therefore underestimate sample size required to detect mortality rate differences between small areas of high larval abundance.

Application to Other Species

A key difference between larval anchovy and most other species of larval fishes is that anchovy are very abundant. The simulation results indicate that surprisingly few positive tows are needed to detect relatively small differences in mortality rates. In the regions considered in the simulation, 50–60% of the tows were positive, and the number of larvae caught per tow averaged 125, with 88% < 10 mm in length. For a less abundant species, the proportion of positive tows and the average number caught per tow would be much lower, and many more tows

would be required to attain the same level of precision.

Application to CalCOFI Surveys

Three key assumptions underlie the use of the CalCOFI time series of larval mortality estimates for hypothesis testing: 1) a stable age distribution prevails (i.e., abundance of several cohorts of larvae at one moment in time is representative of one cohort as it ages through time), 2) variations in observed mortality rate represent true natural variations and not sampling error, and 3) use of the same larval growth parameters for all years does not bias the estimates of mortality rate.

The first assumption was not addressed in this study. It implies negligible immigration and emigration of larvae and continuous production of spawn. The CalCOFI surveys are designed to encompass the anchovy spawning habitat and thus minimize inaccuracies caused by transport of larvae in and out of the survey area. For a species with a broad temporal spawning curve and with repeated spawning by individuals (9–16% of the females spawn each night; table 7, Fiedler et al. 1986), unbiased estimates of mortality rate may be obtained by pooling plankton tows conducted throughout the spawning season (table 6, Hewitt and Methot 1982). With smaller surveys and shorter time periods, the assumption of a stable age distribution may not be suitable, and estimates of mortality rates may be biased.

With regard to the second assumption, our simulations indicate that the time series of daily mortality rate of anchovy larvae represents predominantly real differences owing to biological variation rather than random variation. Recent CalCOFI ichthyoplankton surveys (Table 9) yielded between 36 and 236 positive tows per spawning season. The simulation model indicates that sample sizes >80 are sufficient to detect a difference of 0.5 or more in the mortality coefficient (β) between years (Table 7). When all possible pairs for the eight surveys (1980–87) are compared, 12 of the 28 comparisons had a difference >0.5 (Table 9). Results of our simulation imply that the precision of past surveys was adequate, and the interannual variation in mortality rate (β ranged from 1.22 in 1980 to 2.14 in 1986) is real.

Because larval mortality rate is age-dependent (IMR = β/t) with high mortality occurring during the onset of feeding and decreasing thereafter, variations in daily mortality rates can be typified by "large differences concentrated in a short period of time" and thus be easily detectable (Gulland 1971). The critical issue in comparing mortality rates does not appear to be one of precision but rather one of obtaining a representative sample.

With regard to the third assumption, the simulation also indicated that the risk of introducing a large bias in estimates of mortality rates by using a single family of standard growth curves is relatively low. A large bias would be expected only when the standard growth curves overestimated the actual growth by a factor of two or more. It is unknown how frequently the standard growth curve generates this large bias, for lack of data on variability of larval growth rates from year to year in the field.

TABLE 9.—Number of tows positive for anchovy larvae (n) and mortality coefficients (β) for CalCOFI ichthyoplankton surveys conducted during January through April 1980–87.

Year	n	β
1980	197	1.22
1981	236	1.53
1982	69	1.81
1983	65	2.05
1984	176	1.47
1985	37	2.03
1986	83	2.14
1987	36	1.98

CONCLUSIONS

These simulations validate the use of CalCOFI survey information to test hypotheses regarding larval survival and recruitment (Butler 1987, Peterman et al. 1988). The sample size required for adequate precision of estimates of mortality rates is modest relative to the one required for adequate representation of the spawning season and habitat of a major marine stock such as the northern anchovy. As stated, the critical issue in comparing mortality rates does not appear to be precision of the estimates but rather how well the sample represents the population.

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APPENDIX

Assignment of Larval Ages Using the Pareto Function

The standing stock (SS) of larvae, between the ages of t_h and 20 days, is the integral of the production curve (Fig. 5) over these ages:

$$SS = \int_{t_h}^{20} P_t\,dt = \int_{t_h}^{20} P_h(t/t_h)^{\beta} dt$$

$$= [1 - (20/t_h)^{-(\beta - 1)}] \frac{t_h P_h}{(\beta - 1)} \qquad \text{for } \beta <> 1,$$

$$= [\ln(20) - \ln(t_h)] t_h P_h \qquad \text{for } \beta = 1.$$

Similarly the number of larvae younger than age t is

$$SS_t = [1 - (t/t_h)^{-(\beta-1)}] \frac{t_h P_h}{(\beta - 1)} \qquad \text{for } \beta <> 1,$$

$$= [\ln(t) - \ln(t_n)]\, t_h P_h \qquad \text{for } \beta = 1.$$

The proportion of larvae that are younger than age t is

$$r(t) = SS_t/SS = \frac{1 - (t/t_h)^{(\beta - 1)}}{1 - (20/t_h)^{(\beta - 1)}} \qquad \text{for } \beta <> 1,$$

$$= \frac{\ln(t/t_n)}{\ln(20/t_h)} \qquad \text{for } \beta = 1,$$

where $0 < r(t) < 1$.

By rearranging terms, t can be expressed as

$$t = t_h[1 - r(t)(1 - (20/t_h)^{-(b-1)}]^{-1/(b-1)} \qquad \text{for } b <> 1,$$

$$= t_h(20/t_h)^{r(t)} \qquad \text{for } b = 1,$$

where b is a normal random variable with mean = β and standard error = 0.2 β (0.2 is an arbitrarily chosen value for the coefficient of variation (b) and $r(t)$ is a uniform random variable between 0 and 1).

Sample Allocation

The allocation of tows to each region and month was based on the 1984 sampling pattern (Table 2, Fig. 2). For a total of N tows, the number of positive tows allocated to month i and region j was computed as

$$n(i,j) = N * p(i) * q(j|i) * r(j|i)$$

where $p(i)$ is the proportion of tows for month i and $\Sigma p(i) = 1$
$q(j|i)$ is the proportion of tows made in region j during month i and $\Sigma q(j|i) = 1$
$r(j|i)$ is the proportion of positive tows for region j during month i and $0 <= r(j|i) <= 1$.

A uniform random number generator was used to assign each tow to a month and region, to determine whether the tow was positive or not, and thus to produce $n(i,j)$.

Assignment of the Time of Tow

Table 3 lists parameters for Gamma distributions fitted to the actual time between positive tows minus the minimum time between any two positive tows (i.e., plankton tows which caught at least one anchovy larva) in each region because the Gamma distribution takes all values to be greater than zero. Each distribution is shifted to the right by the constant listed (the minimum time between any two positive tows). Actual times greater than 150 hours were assumed to be periods of transit to and from port and were thus excluded when fitting the distributions.

The time of the first tow of a simulated survey was chosen randomly and incremented by time intervals selected from the distributions described in Table 3. If the selected time interval was greater than 4 hours, tows with zero catch were inserted. The number of zero tows inserted was the time interval between two positive stations divided by the average travel time between stations (2 hours).

Catchability, Growth, and Mortality of Larval Fishes

Wallace W. Morse

ABSTRACT: The catchability of fish larvae with a 61 cm bongo net was determined from analysis of day, night, and twilight samples from 8,312 stations made off the northeast United States during 1977–84. Night catches exceeded day catches by 62% and twilight exceeded day catches by 44%. Catchability by year and month revealed some variations; however, night catches still dominated. The daily cycle in catchability of all larvae showed that the maximum catch occurred at approximately 0200, and was about 2.5 times the minimum catches at 1700. Changes in catchability with water column depth reflected changes in species composition of the catches.

Analysis of 36 taxa revealed 11 significant differences in day:night, day:twilight, and night:twilight catch ratios. Length-dependent catchability and correction factors were determined for 26 species. Corrected length frequencies were used to calculate length-dependent mortalities which are shown to be positively correlated with water temperature. Larval growth rates were also found to be temperature dependent and, by incorporating a length-weight coefficient, larval length was converted to age. Age-frequencies were used to calculate daily larval mortality and, for most species, the ratio of mortality rate to growth rate was approximately 0.8. Those species with ratios at or over 1.0, i.e., bluefish, *Pomatomus saltatrix*; *Sebastes* spp.; Atlantic mackerel, *Scomber scombrus;* cunner, *Tautogolabrus adspersus*; and, to some extent, haddock, *Melanogrammus aeglefinus*, probably exhibit significant net avoidance.

Surveys of ichthyoplankton in the marine environment have been an integral part of fisheries science for nearly a century. Today large marine ecosystems are routinely monitored for both physical and biological parameters to study multispecies interactions during the early life history of fishes (Sherman 1986). One of the major goals of large marine ecosystem surveys is to monitor the inter- and intra-annual changes in larval fish abundance and mortality and their relationship to recruitment of fishable biomass.

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Fishery Bulletin, U.S. 87: 417–446.

Demonstrating the relationship between larval abundance and recruitment has remained elusive owing, in part, to the complexities of the interactions of the physical and biological factors that affect survival of fish during the first year of life. However, a number of theories have been proposed that attempt to link larval fish survival and, by inference, recruitment with their food supply. These include the "critical period" theory (Hjort 1914; May 1974), the "match-mismatch" theory (Cushing 1975), and the mixed layer stability hypothesis (Lasker 1981).

A requisite condition for the testing of these and other theories using broadscale ichthyoplankton surveys is what Zweifel and Smith (1981) call an "effective sampler size". This involves accounting for the "effect of environmental and behavioral factors on the content of the samples or collections". The objective of accounting for these factors is to standardize the sampling gear by applying correction factors in order to minimize sampling variability and to make samples comparable (Smith and Richardson 1977). A key consideration and a possible serious source of bias in larval fish collections is net avoidance (Clutter and Anraku 1968). Fish larvae can avoid capture by swimming out of the path of an approaching net or by migrating below the maximum depth sampled by the net. If detection of an approaching net by larvae is visual, changes in light intensity or net coloration will alter catchability. The magnitude of visually cued avoidance is indicated by the variation in day versus night catches.

Differences in day versus night catches for numerous species have been reported for the past 60 years (e.g., Johansen 1925; Russell 1926; Ahlstrom 1954; Bridger 1956; Miller et al. 1963; Lenarz 1973). In most cases night catches exceed day catches. But there is evidence that gear configuration and towing speed affect the ratio of day-to-night catches (Bridger 1956; Clutter and Anraku 1968). For example, Miller et al. (1963) attributed the lack of difference in day-to-night catches of haddock, *Melanogrammus aeglefinus*, to the high speed (4 m/s) gear they used.

Accounting for the various sources of sampling bias and for standardizing larval catches facilitates the calculation of the critical population parameters of abundance and mortality. These parameters are the basis for testing the possible effects of biotic and abiotic variables upon larval fish survival and recruitment and are often used to support or reject a particular hypothesis. The general effect of net avoidance is an increase in estimates of mortality (Clutter and Anraku 1968), which in turn can lead to unrealistic conclusions.

The interrelationship of mortality and growth parameters has been firmly established for fishes in the marine ecosystem (Beverton and Holt 1957; Ursin 1967; Ware 1975; Shepherd and Cushing 1980; Peterson and Wroblewski 1984; Houde 1987; and others). The underlying assumptions for this relationship are that mortality is the result of predation and that predation rates decrease as prey size increases. This simplistic model was described as the "cube root rule" (Ursin 1967) where mortality is equal to the cube root of the weight. Peterson and Wrobleski (1984) expanded this relationship to include growth efficiency and metabolism and estimated the annual mortality rate (M) for larval and adult fishes weighing between 10^{-5} and 10^{3} g as $M = (1.92 * \text{year}^{-1})\ \text{weight}^{-25}$. Pauly (1980) noted the rather weak relationship between fish size and mortality ($r^2 = 0.38$) and found that the inclusion of environmental temperature significantly improved the fit ($r^2 = 0.71$) of mortality to maximum length and growth rate for 175 fish stocks. The objectives of this study are to determine the changes in larval fish catches during day, night, and twilight hours and provide correction factors to standardize catches for net avoidance. These corrections can significantly change the abundance and mortality estimates of those species that show a difference in day, night, or twilight catches. Length-dependent larval mortality is estimated from avoidance-corrected abundances for 26 fish taxa and is related to water temperatures. The relationships of larval growth, mortality, and water temperature are explored to determine if net avoidance is, in fact, a serious problem as it relates to estimtes of larval mortality.

METHODS

Continental shelf and slope waters off the northeast United States have been sampled six to eight times each year since 1977 to provide information on the distribution and abundance of fish eggs and larvae as well as to provide fisheries independent estimates of spawning biomass. A total of 8,312 stations were occupied from 1977 through 1984 between Cape Hatteras, NC, and Nova Scotia (Fig. 1). At each station a 61 cm bongo net frame, fitted with 505 μ and 333 μ mesh nets and flowmeters, was lowered at 50 m/min to within 5 m of the bottom or to 200 m maximum and retrieved at 20 m/min. Ship speed was adjusted to maintain a wire angle of 45 degrees; the 505 μ mesh net was used for ichthyoplankton analysis; and samples were preserved in 5% formalin. All fish larvae were identified to the lowest taxon possible, enumerated, and measured to the nearest 0.1 mm standard or notochord length. If more than 50 specimens of a particular taxon were captured in a tow, then 50 randomly selected larvae were measured. Water temperature profiles were taken at each station. A detailed account of all shipboard and laboratory methods, and sampling locations is provided in Sibunka and Silverman (1984).

Larval catches were standardized (S) to the number under 10 m^2 of sea surface by the equation:

$$S = 10 * N * D * A^{-1} * M^{-1} \qquad (1)$$

where N is the number of larvae in the sample, D is the maximum depth of the tow in meters, A is the area of the mouth of the net, and M is the distance the net was towed in meters determined from the calibrated flowmeter (Smith and Richardson 1977). All analyses followed standardizing of catches to the number of larvae under 10 or 100 m^2 and rounding of lengths to the nearest mm.

Each station was assigned to day, night, or twilight hours according to the recorded time at the beginning of the tow. Twilight was designated as one hour before and after both sunrise and sunset while day or night was assigned between the two twilight intervals.

Catches of all larvae were analyzed by hour of the day to determine if a daily cycle in catchability could be detected. The assumption in this analysis is that the daily cycle of incident light is the controlling factor for visual detection of the net. The seasonal and latitudinal changes in the duration of daylight hours (e.g., 8.6 hours in winter to 15.4 hours in summer) made it necessary, in order to maintain equivalent light regimes across seasons and areas in the analysis, to partition the day into 24 intervals of 10 for

daylight, 10 for nighttime, and 2 for each of the twilight times. The number of hours (H) between sunrise and sunset for each station was calculated using latitude and Julian day (Iqbol 1983), as follows

$$H = -7.6393 * \arcsin[\sin(L) * \sin(C)/(\cos(L) * \cos(C))]$$

where $L = 0.0172$(latitude).

$$C = 0.3964 - 22.9133 * \cos(Z) + 4.1580 * \sin(Z) - 0.3964 * \cos(2Z) + 0.5197 * \sin(2Z) - 0.1545 * \cos(3Z) + 0.0848 * \sin(3Z), \text{ and}$$

$$Z = 0.0172 \text{ (Julian day } -1).$$

Twilight hours remained one hour before and after sunrise and sunset and were partitioned into hour intervals 5–6 and 17–18, respectively, and accounted for 4 of the 24 h day. The remaining daylight hours ($H - 2$), where H is time from sunrise to sunset, were partitioned into 10 equal intervals (i.e., hours 7–16). Nighttime hours ($24 - (H + 2)$) were also partitioned into 10 intervals corresponding to hours 0–4 and 19–23. The time interval for a daylight "hour" ranged from about 52 minutes in winter to 92 minutes in summer. Each station was assigned an "hour" interval and analysis was performed during this interval.

The occurrence of tows that did not contain larvae or that did not contain the particular taxon of interest presented a special problem in day-versus night-catch analysis. The absence of larvae might have occurred because there were no larvae within the path of the net or because of net avoidance by the larvae. This being the case, all stations in cruises that contained at least one occurrence of the taxon being investigated, except where noted, were included in calculations of mean catch per 10 m^2. The result of including these zero tows was a reduction in the mean catch, but a stability in the catch ratios. In addition, the survey area was divided into four subareas: Middle Atlantic Bight (MAB), Southern New England (SNE), Georges Bank (GB), and Gulf of Maine (GOM) (Fig. 1). The subareas were used to stratify the entire survey area during analysis for those taxa that spawn in a limited area. For example, if no larvae of a particular species were caught in GOM subarea then all GOM stations were ignored for the analysis of that species. The calculation of the mean catch and its variance using zero tows followed the methods of Pennington (1983) for the Delta distribution of catch frequencies. Ratios of all larvae for day, night, and twilight were based on mean catch per 10 m^2, and ratios for millimeter length increments were based on mean catch per

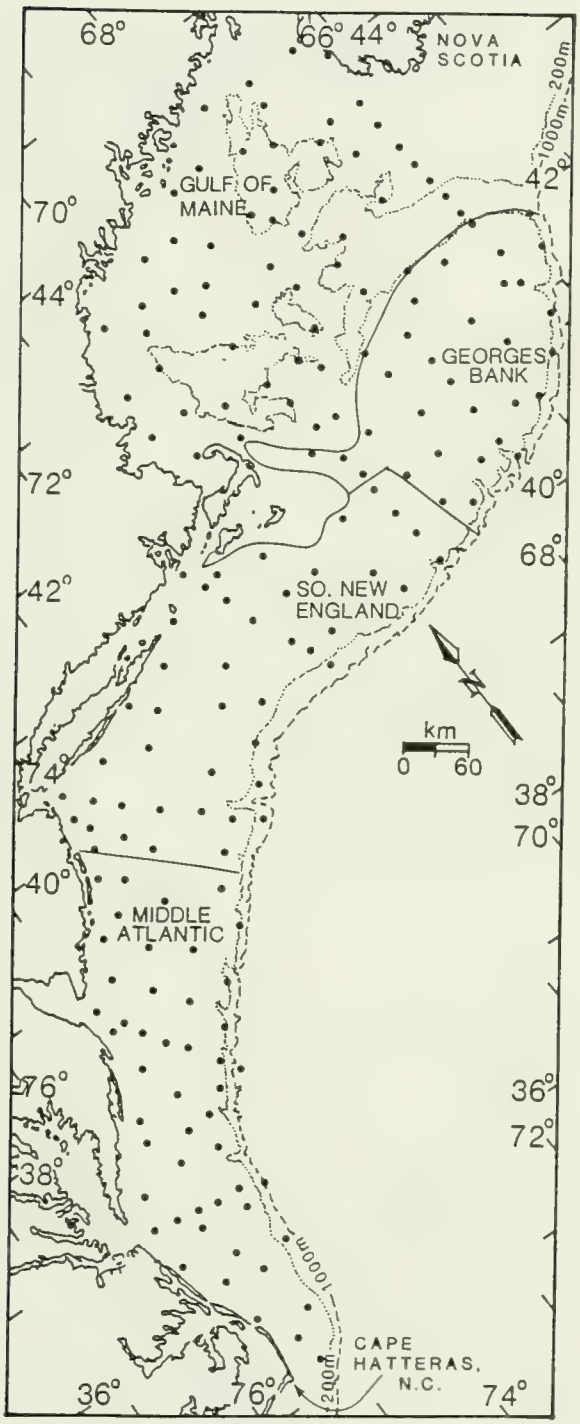


FIGURE 1.—Map of area surveyed, station locations and subareas off the northeast United States.

100 m^2. Other statistics were calculated according to Zar (1984).

The analysis to derive correction factors for day, night, and twilight catchability and to derive estimates of larval mortality for 26 species involved three steps. The larval length-interval used was calculated from the modal length, which was always greater than the minimum length captured, to the maximum length that was captured in all three light regimes. I assumed that the modal length was the minimum length fully retained by the 505 μ mesh net. If extrusion of larvae at modal lengths or greater is significant, length-dependent mortalities will be underestimated and will have no effect on catch ratios. The exponential decay regression model was fitted to the larval length (X_i) and catch per 100 m^2 (Y_i) as

$$Y_i = \alpha \exp(-\beta X_i) + \epsilon_i \quad (2)$$

for each species by day, night, and twilight catches. The expected catches from these regressions were then used to estimate the ratios of catch by length for night:day and twilight:day. The predictive nonlinear second-order polynomial regression model:

$$R_i = \alpha + \beta_i X_i + \beta_1 X_i^2 + \epsilon_i \quad (3)$$

was fitted to the ratios by length. (The predicted ratio (R_i) of night:twilight catches for any length (X_i) is, of course, the ratio of night:day at X_i divided by the twilight:day ratio at X_i.) The catches at each length per 100 m^2 were then corrected using the predicted ratios that maximized the catches. The exponential decay model was again fitted to the corrected catches and the slope of the line was used as an estimate of length-dependent mortality.

RESULTS

All Larvae

The initial analysis examined the catches for all taxa combined for all 8,312 stations, of which 6,530 contained fish larvae. The mean catch per 10 m^2 was calculated for 3,578 day stations, 3,332 night stations, and 1,402 twilight stations (Table 1). A significant difference ($P < 0.05$) was found between night-versus-day and night-versus-twilight catches with the ratios of the mean catches of 1.62:1 and 1.44:1, respectively. The combining of all data raises the question of whether one or more year's data might have been anomalous and produced the significant difference in catches. Each year was analyzed separately and is shown in Table 1. For each year the highest mean catches always occurred at night and in six of the eight years twilight catches exceeded day catches. In four of the eight years a significant difference ($P < 0.05$) was found between night and day catches (1977, 1982–84). The consistent interannual relationships in catches indicate that the combined years' ratios are good indicators of average catchability of all larvae during the 8 yr study.

The analysis of the combined data-set integrates the areal and temporal heterogeneity in the distribution and abundance inherent within the larval fish community. To determine if the

TABLE 1.—The mean catch per tow (#/10 m^2) by day, night, and twilight of fish larvae collected off the northeast United States for years 1977–84 and combined. Numbers in parenthesis are standard error of the mean and sample size. Values of Student *t* test for differences in mean catches.

Year	Day (D)	Night (N)	Twilight (T)	*t*-value		
				D vs. N	D vs. T	N vs. T
1977	162.868(20.774,591)	260.308(34.274,555)	206.796(46.380,209)	2.4649*	0.9871	0.8536
1978	143.513(22.610,434)	197.502(34.681,401)	121.823(27.723,178)	1.3233	0.5488	1.3698
1979	159.847(19.779,410)	228.784(34.595,178)	170.466(32.641,153)	1.7871	0.2793	1.0248
1980	154.223(20.147,455)	241.296(35.886,397)	187.856(40.815,164)	2.1845	0.8096	0.8661
1981	195.026(27.800,426)	264.761(36.220,412)	178.697(33.435,180)	1.5336	0.3403	1.4562
1982	127.302(18.571,372)	237.059(37.154,366)	126.952(28.913,154)	2.6552*	0.0102	1.8262
1983	134.868(20.838,401)	265.698(47.486,396)	215.808(57.246,172)	2.5379*	1.6468	0.6142
1984	145.628(18.225,489)	287.115(41.634,452)	169.497(32.560,192)	3.1947**	0.6719	1.7468
All	155.379(7.948,3578)	251.673(14.582,3332)	174.533(13.931,1402)	5.9058**	1.2435	3.1837**

* = $P < 0.05$.
** = $P < 0.01$.

ratios of day, night, and twilight catches show seasonal or areal differences, separate ratios of the mean catch per 10 m^2 were calculated for each month for all subareas and by subarea (Table 2). In all months the ratios of night-versus-day catches for all subareas combined were greater than one. Night-to-day ratios ranged from 1.01 in September to 3.23 in January and the mean for all months was 1.82 (SD = 0.56). The extreme values in January and September may be related to the relatively low sample sizes for these two months; however, the higher catches at night relative to both day and twilight catches remained quite consistent regardless of month.

Considerably more variability in the ratios between months is evident when each subarea is analyzed separately, but the general trend of dominance in night catches is still evident within each subarea. The extraordinarily low ratio for twilight-versus-day catches for January in the Gulf of Maine results from a few extremely high twilight catches and relatively low sampling intensity (N = 17).

Catches of all larvae grouped by water column depth are shown in Figure 2. They peak at

TABLE 2.—Ratios of night (N):day (D) and twilight (T):day (D) mean catches of larval fish caught off the northeast United States, 1977–84, by subarea and combined by month. n = number of samples; MAB = Middle Atlantic Bight; SNE = Southern New England; GB = Georges Bank; GOM = Gulf of Maine.

	All			MAB		SNE		GB		GOM	
Month	n	N/D	T/D	N/D	T/D	N/D	T/D	N/D	T/D	N/D	T/D
Jan.	166	3.23	0.37	—	—	—	—	1.47	0.58	1.85	0.07
Feb.	536	1.92	1.15	2.38	1.00	0.81	0.68	1.19	1.25	2.70	4.35
Mar.	906	1.51	1.02	1.33	0.86	1.47	1.39	0.90	0.41	0.47	1.92
Apr.	897	1.45	0.96	2.13	1.75	1.56	1.12	1.15	0.56	0.59	0.45
May	1,112	1.49	1.11	1.10	0.56	1.88	1.64	1.52	1.23	1.28	1.69
June	727	2.43	1.16	2.63	0.79	1.89	1.27	1.01	1.30	3.23	0.99
July	690	2.00	1.06	2.86	1.47	1.20	0.84	7.69	1.75	1.09	0.46
Aug.	850	1.69	1.32	1.25	1.89	2.50	1.19	1.47	1.33	1.35	0.84
Sept.	277	1.01	0.83	1.24	0.79	0.99	—	—	—	—	—
Oct.	1,015	1.75	1.04	0.94	0.42	1.75	1.61	1.85	1.45	2.00	0.56
Nov.	654	1.69	1.85	0.68	0.66	2.01	2.13	1.85	0.43	4.54	7.14
Dec.	482	1.68	1.64	—	—	0.76	1.79	3.23	6.25	4.76	0.91

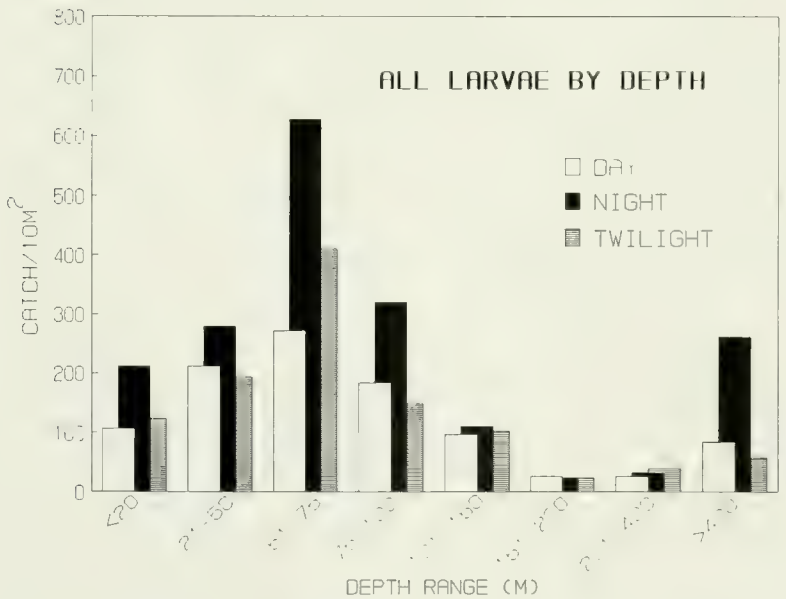


FIGURE 2.—Mean catch of all larvae by bottom depth interval for day, night, and twilight.

depths between 51 and 75 m, decrease to a low at 151–200 m, and then increase again at depths >400 m. The increase in catch per tow at the deep water stations is due to the dominance of two mesopelagic lantern fishes, *Ceratoscopelus maderensis* and *Benthosema glaciale*, which account for 47% of all larvae at these depths. Night catches exceeded day and twilight catches except between 101 and 400 m. At these water column depths the dominant taxa are *Sebastes* spp.; silver hake, *Merluccius bilinearis*; offshore hake, *Merluccius albidus*; Gulf Stream flounder, *Citharichthys arctifrons*; *Urophycis* spp.; Atlantic herring, *Clupea harengus*; and *Ammodytes* spp., all of which comprise 71% of the total catch. The twilight catch at column depths between 101 and 150 m exceeds both the night and day catches and reflects the high twilight catches for Gulf Stream flounder, offshore hake, and to some extent butterfish, *Peprilus triacanthus*.

The daily cycle in mean catch per 10 m^2 for all larvae is shown in Figure 3a. Catches were highest between hour intervals 1 and 6, with maximum catches at hour 2. Minimum catches occurred between intervals 10 and 17 and averaged only 39% of the catch at interval 2. The ratios of the catch at each hour interval, divided by the

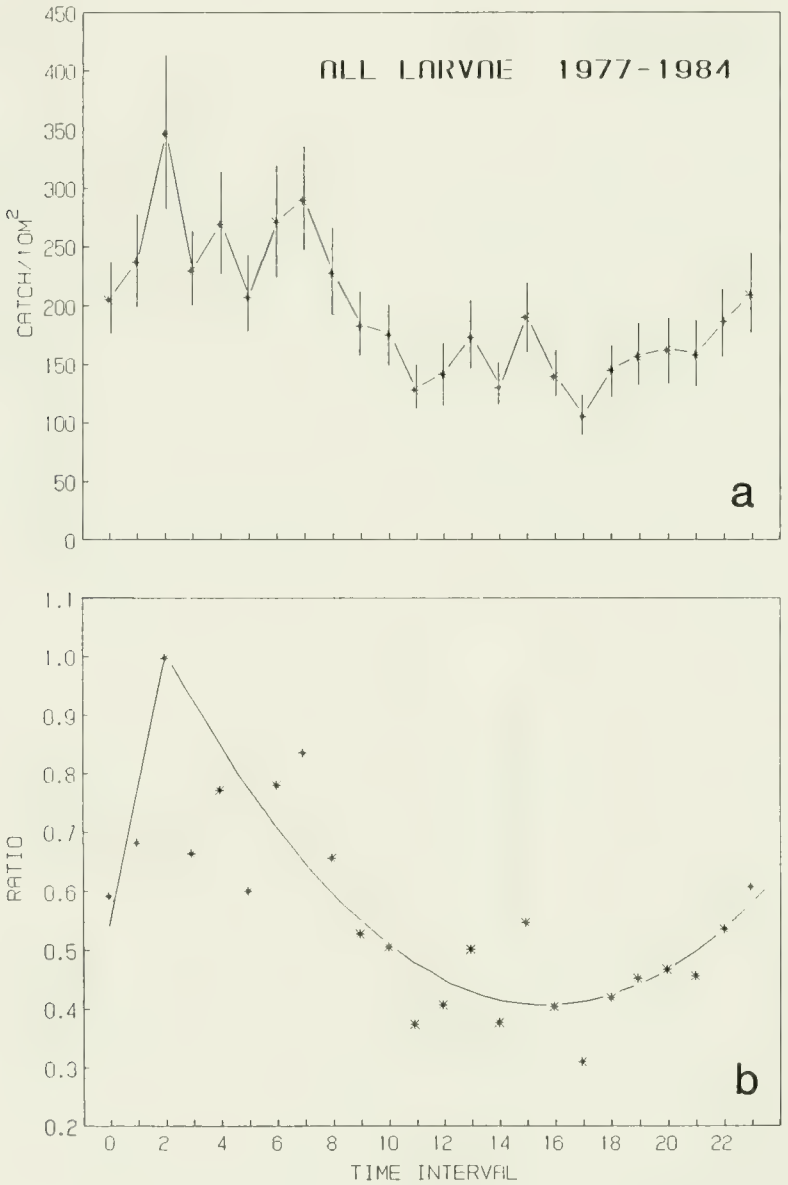


FIGURE 3.—Mean catch per 10 m^2 by time intervals and standard error bars and plot of ratios of catch at time interval 2 with the fitted curves.

catch at hour 2, yield a correction factor to standardize the catch of all larvae for net avoidance. Two linear functions were fit to the ratios for hour intervals 0–2 and intervals 2–23 for the purpose of calculating the correction factor to account for the daily cycle in catches (Fig. 3b).

The equations are

$$C = 0.5575 + 0.2025 * H$$
$$r^2 = 0.91 \quad n = 3 \quad \text{for } H < 3$$

$$C = 1.1992 - 0.1012 * H + 0.00323 * H^2$$
$$r^2 = 0.81 \quad n = 21 \quad \text{for } H > 2$$

where C = the correction factor and H = the hour interval.

Individual Taxa

A total of 36 taxa, representing 17 families, were analyzed for day, night, and twilight catches based upon their abundance within the data set. These taxa represented fewer than 11% of all taxa caught during the 8 yr study but account for over 90% of all larvae captured. They were selected because their abundance is adequate for statistical comparisons of catches. Of the 36 taxa, four were identified to the generic level due to the uncertainty of species identifications, the rest to the specific level. Table 3, a phylogenetic listing (Robins et al. 1980) of the catch data, analyzes the variance (ANOVA) of the delta mean catch per 10 m^2 for each of the 36 taxa by day, night, and twilight and presents Tukey tests of paired means when the ANOVA showed significant differences. The ANOVA showed that the catches of 11 of the 36 taxa have significant differences: day versus night for 9 taxa, day versus twilight for 1 species, and night versus twilight for 7 species. It is interesting to note that the first three taxa listed in Table 3, i.e., the top of the phylogenetic list, contain 25% of all the significant differences found.

In a review of larval swimming needs, Theilacker and Dorsey (1980) showed that jack mackerel, *Trachurus symmetricus*; Pacific mackerel, *Scomber japonicus*; and herring, *Clupea harengus* (two short-bodied and a long-bodied morph) are fast swimmers while sardine, *Sardina pilchardus*; and northern anchovy, *Engraulis mordax* (two long-bodied larvae) are slow swimmers. The implication is, of course, that fast swimming larvae will avoid the approaching net and are most likely to show differences between day and night catches. The larvae of Atlantic menhaden, *Brevoortia tyranus*; Atlantic herring, *C. maderensis*; and *Ammodytes* spp. are long-bodied, while *B. glaciale*; Atlantic mackerel, *Scomber scombrus*; and *Auxis* spp. are short-bodied. At this point no clear relationship seems evident between general morphology and net avoidance; in fact, the results of this study appear counterintuitive.

The occurrences of the 11 significant differences shown in Table 3 are surprising, given the length frequencies of most species considered. The dual effects of larval mortality and net avoidance produce an exponential decline in the abundance of larvae with increasing length. This results in a concentration of larval abundance in the smallest length intervals (usually 3–7 mm), which should be the lengths that are least able to avoid the net. Because of the preponderance of small larvae in the catches, the mean catch per 10 m^2 most reflects the abundance of these small larvae, and thus the statistical significance or insignificance of the differences in catches may not reveal the changes in catchability with increasing larval length. It is interesting to note that 29 of the 36 taxa (81%) show higher night catches than day catches, though statistical significance is met in only 9 taxa.

The changes in catchability with length were investigated by calculating the mean catch per 100 m^2 for each mm length-increment by day, night, and twilight for 26 taxa (Fig. 4). The range of lengths for each species does not show the entire length range captured; rather, they show sequential lengths where positive day, night, and twilight catches were made. For example, *Ammodytes* spp. were captured during day, night, and twilight between lengths 3 and 32 mm but the total length range represented in the 8 yr data set is 1–141 mm. Obviously a mean catch-per-tow of zero cannot be corrected for net avoidance and is therefore not considered in this analysis.

The most common ratios of catches, and the most easily explained in terms of visual net avoidance, are night equals or exceeds day catches, with increasing ratios as larval length increases. The ratios for each length of night:day for expected catches from the regression analysis follow this pattern for 17 of the 26 species analyzed. The magnitude of the difference between night and day varies greatly between species, but the general trend is clearly evident in all 17 species. The only species that shows day catches exceeding night catches at all lengths is

TABLE 3.—Mean larval fish catches per 10 m^2 for day, night, and twilight made off the
significant differences. Numbers in parenthesis

Taxa	Day (D)	Night (N)
Brevoortia tyranus[1] Atlantic menhaden	0.656(0.180,847)	3.434(1.036,861)
Clupea harengus[2] Atlantic herring	3.943(0.941,1314)	10.048(1.846,1589)
Ceratoscopelus maderensis[3]	0.982(0.181,1759)	5.652(0.925,1532)
Benthosema glaciale	1.725(0.305,2201)	2.066(0.329,1928)
Lophius americanus Goosefish	0.621(0.052,2543)	0.488(0.053,1994)
Urophycis spp. hakes	21.505(2.221,2668)	25.563(2.967,2294)
Enchelyopus cimbrius Fourbeard rockling	0.694(0.073,2675)	0.838(0.103,2327)
Gadus morhua Atlantic cod	2.441(0.285,2813)	2.218(0.248,2685)
Melanogrammus aeglefinus[3] Haddock	6.250(1.031,1456)	4.838(1.058,1211)
Pollachius virens[2] Pollock	0.683(0.095,1961)	1.083(0.141,2044)
Merluccius albidus Offshore hake	1.289(0.216,1838)	1.662(0.315,1597)
Merluccius bilinearis Silver hake	13.442(1.408,2514)	15.814(1.794,2239)
Centropristis striata[1] Black seabass	1.151(0.186,1274)	1.841(0.334,955)
Pomatomus saltatrix[1] Bluefish	16.212(2.814,931)	25.967(6.050,585)
Cynoscion regalis[1] Weakfish	0.894(0.230,908)	1.515(0.487,695)
Micropogonias undulatus[1] Atlantic croaker	5.083(2.144,893)	4.806(1.733,812)
Tautogolabrus adspersus Cunner	3.778(0.518,1363)	8.557(1.528,966)
Tautoga onitus[1] Tautog	0.337(0.079,761)	0.688(0.251,498)
Lumpenus lumpretaeformis[3] Snakeblenny	0.500(0.145,700)	0.250(0.070,581)
Ulvaria subbifurcata[3] Radiated shanny	0.462(0.152,633)	0.656(0.185,401)
Pholis gunnelus Rock gunnel	0.405(0.085,1245)	0.564(0.090,1164)
Ammodytes spp. Sand lances	48.001(5.311,2267)	125.737(15.608,2125)
Auxis spp. Mackerels	2.326(0.500,590)	7.549(1.838,397)
Scomber scombrus Atlantic mackerel	18.195(4.133,1284)	35.886(10.866,772)
Peprilus triacanthus Butterfish	5.299(0.507,2566)	6.025(0.716,2019)
Sebastes spp.[3] Redfishes	2.276(0.295,1541)	3.006(0.467,1169)
Myoxocephalus octodecemspinosus Longhorn sculpin	0.249(0.056,707)	0.699(0.132,731)
Citharichthys arctifrons[2] Gulf Stream flounder	16.288(1.882,1970)	19.577(2.511,1620)
Etropus microstomus[1] Smallmouth flounder	5.977(0.755,1658)	7.873(1.125,1339)
Paralichthys dentatus[2] Summer flounder	1.795(0.262,1458)	2.135(0.260,1554)
Paralichthys oblongus[2] Fourspot flounder	8.089(0.689,1691)	7.578(0.785,1324)
Scophthalmus aquosus[2] Windowpane flounder	2.694(0.246,2174)	3.348(0.319,1864)
Hippoglossoides platessoides[3] American plaice	1.580(0.427,989)	1.268(0.276,700)

northeast United States during 1977–85 and analysis of variance (F) and Tukey (q) tests for are standard error of the mean catch and sample size.

Taxa	Twilight (T)	F value	q		
			D:N	D:T	N:T
Brevoortia tyranus[1] Atlantic menhaden	2.072(1.079,340)	3.542*	**	—	—
Clupea harengus[2] Atlantic herring	7.137(2.276,620)	3.898**	**	—	—
Ceratoscopelus maderensis[3]	2.125(0.636,642)	15.928**	**	—	*
Benthosema glaciale	1.781(0.392,838)	0.328			
Lophius americanus Goosefish	0.508(0.073,920)	1.814			
Urophycis spp. hakes	28.091(5.008,991)	1.085			
Enchelyopus cimbrius Fourbeard rockling	0.707(0.126,1008)	0.760			
Gadus morhua Atlantic cod	1.552(0.260,1106)	1.776			
Melanogrammus aeglefinus[3] Haddock	3.967(0.961,550)	0.982			
Pollachius virens[2] Pollock	0.705(0.141,813)	3.361*	*	—	—
Merluccius albidus Offshore hake	3.284(0.842,682)	5.584**		**	*
Merluccius bilinearis Silver hake	12.235(1.940,964)	0.977			
Centropristis striata[1] Black seabass	0.857(0.256,433)	3.020*	—	—	*
Pomatomus saltatrix[1] Bluefish	10.948(3.418,313)	2.467			
Cynoscion regalis[1] Weakfish	0.981(0.313,331)	0.922			
Micropogonias undulatus[1] Atlantic croaker	0.842(0.348,327)	0.838			
Tautogolabrus adspersus Cunner	4.217(1.052,467)	6.633**	**	—	*
Tautoga onitus[1] Tautog	0.527(0.223,244)	1.275			
Lumpenus lumpretaeformis[3] Snakeblenny	0.272(0.147,273)	1.307			
Ulvaria subbifurcata[3] Radiated shanny	0.436(0.224,192)	0.403			
Pholis gunnelus Rock gunnel	0.482(0.119,494)	0.862			
Ammodytes spp. Sand lances	71.144(10.956,896)	13.376**	**	—	**
Auxis spp. Mackerels	2.091(0.891,194)	6.901**	**	—	*
Scomber scombrus Atlantic mackerel	15.607(5.899,410)	2.128			
Peprilus triacanthus Butterfish	5.741(0.918,915)	0.372			
Sebastes spp.[3] Redfishes	1.985(0.350,560)	1.580			
Myoxocephalus octodecemspinosus Longhorn sculpin	0.324(0.122,329)	4.853**	**	—	—
Citharichthys arctifrons[2] Gulf Stream flounder	21.337(4.178,703)	0.943			
Etropus microstomus[1] Smallmouth flounder	3.921(0.947,589)	2.946			
Paralichthys dentatus[2] Summer flounder	1.872(0.402,600)	0.452			
Paralichthys oblongus[2] Fourspot flounder	7.705(1.235,597)	0.125			
Scophthalmus aquosus[2] Windowpane flounder	3.647(0.626,787)	1.928			
Hippoglossoides platessoides[3] American plaice	2.614(1.237,329)	1.093			

TABLE 3.—*Continued.*

Taxa	Day (D)	Night (N)
Glyptocephalus cynoglossus Witch flounder	0.908(0.080,2716)	0.987(0.120,2122)
Limanda ferruginea Yellowtail flounder	5.488(0.510,2110)	8.241(0.963,1492)
Pseudopleuronectes americanus Winter flounder	0.358(0.063,1317)	0.561(0.116,907)

* = $P < 0.05$.
** = $P < 0.01$.
[1]samples from Middle Atlantic Bight and Southern New England subareas.
[2]samples from Middle Atlantic, Southern New England, and Georges Bank subareas.
[3]samples from Southern New England, Georges Bank, and Gulf of Maine subareas.

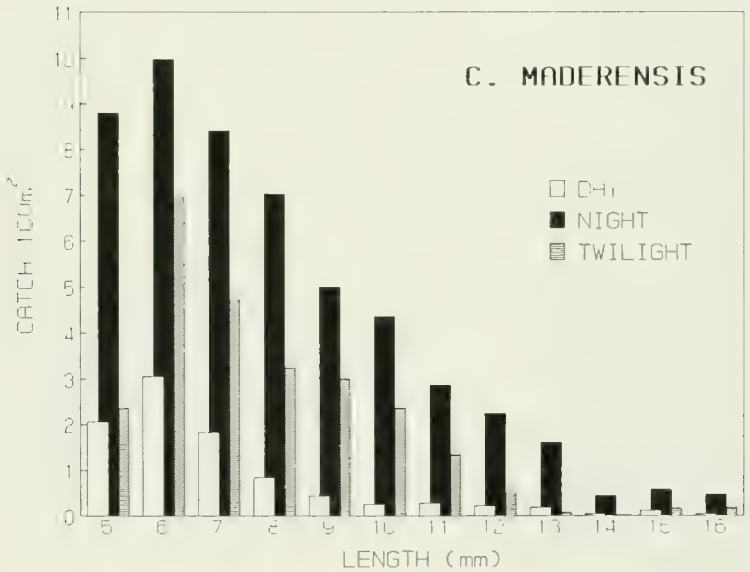
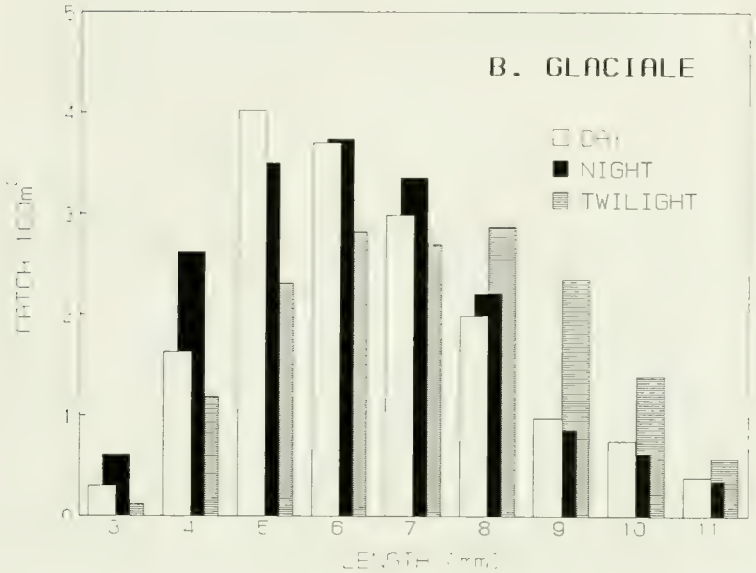
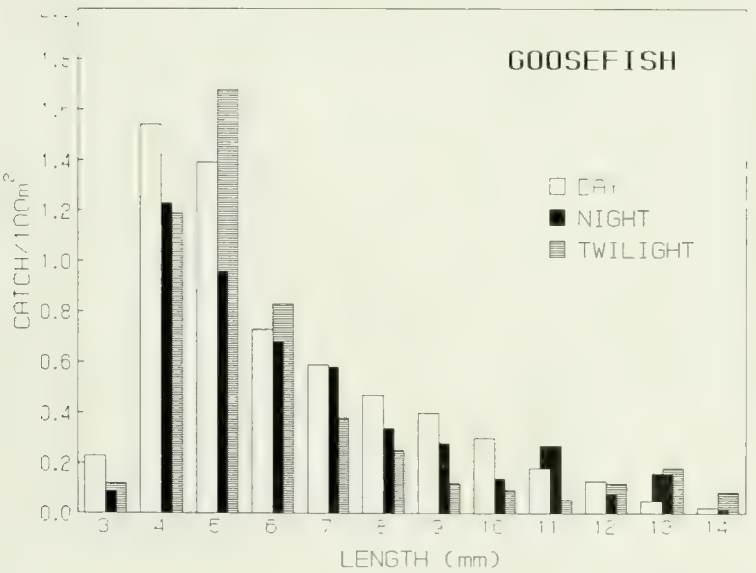


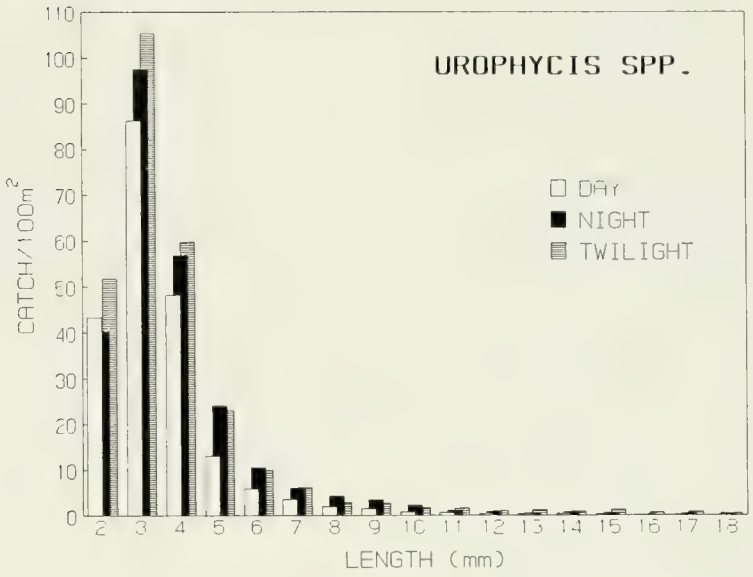
FIGURE 4 a–g.—Plots of mean catch per 100 m^2 by length for day, night, United States,

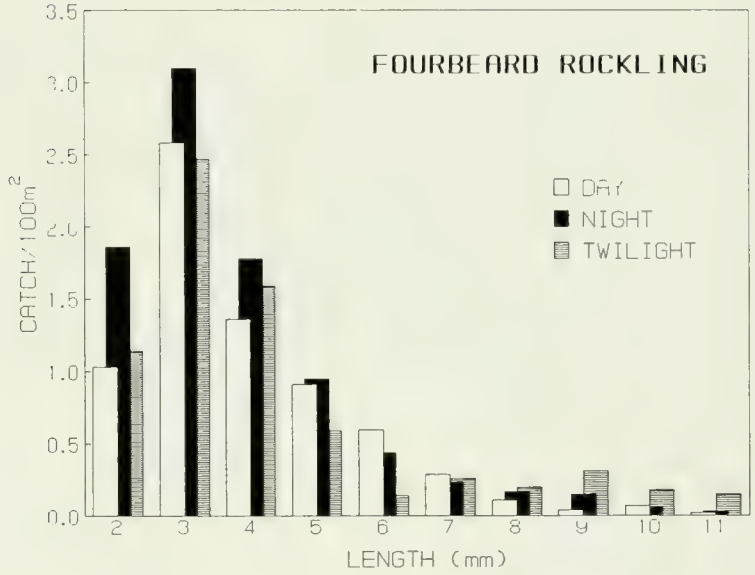
Taxa	Twilight (T)	F value	q D:N	q D:T	q N:T
Glyptocephalus cynoglossus Witch flounder	0.702(0.102,974)	1.297			
Limanda ferruginea Yellowtail flounder	5.589(0.972,706)	4.237*	**	—	·
Pseudopleuronectes americanus Winter flounder	0.388(0.127,453)	1.460			





and twilight for 26 taxa of fish larvae collected off the northeast 1977–84.





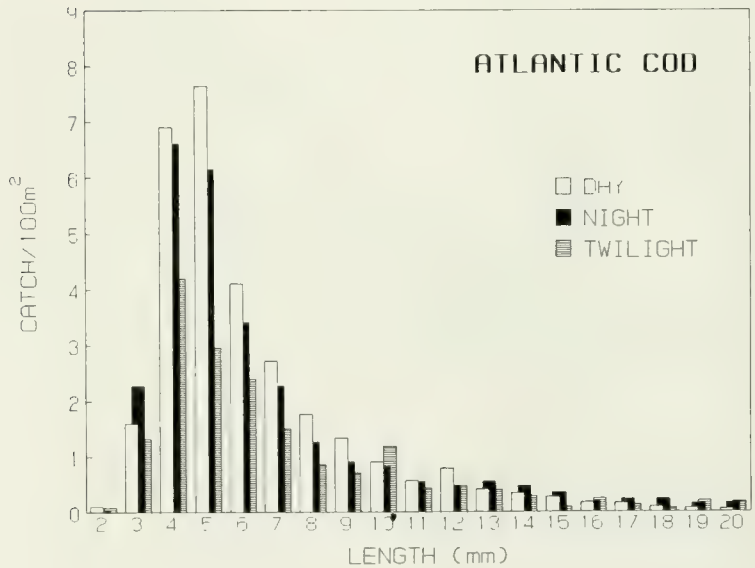
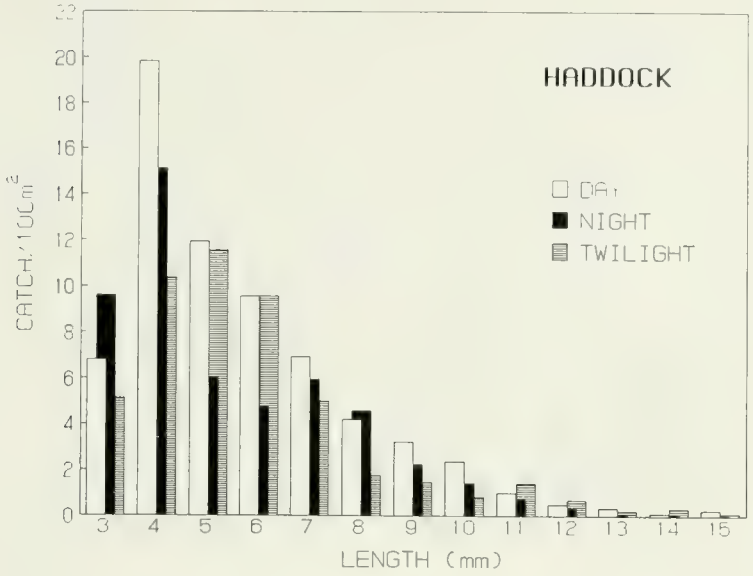
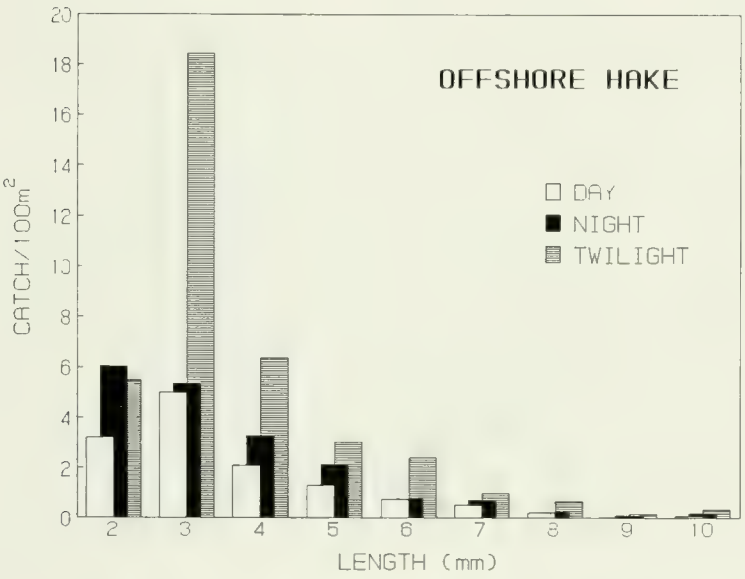
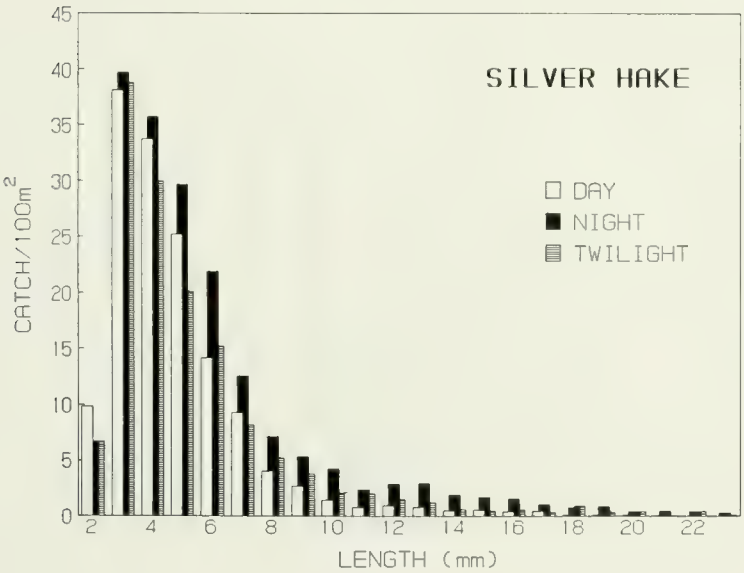
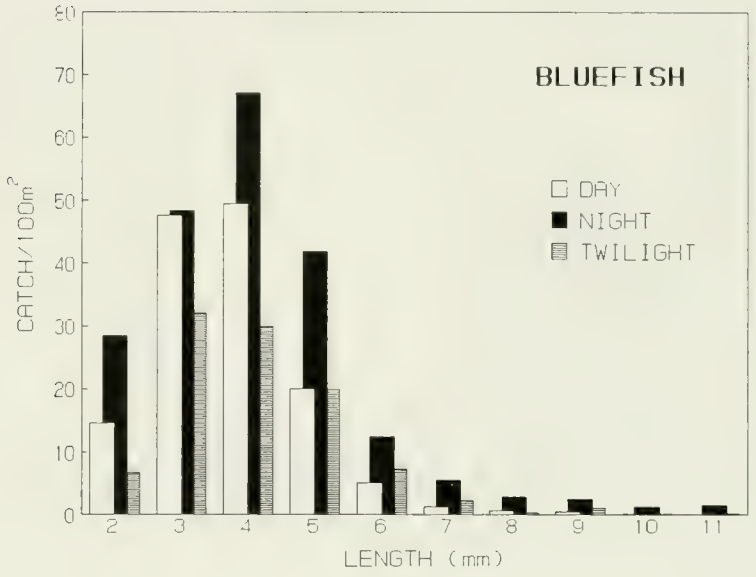


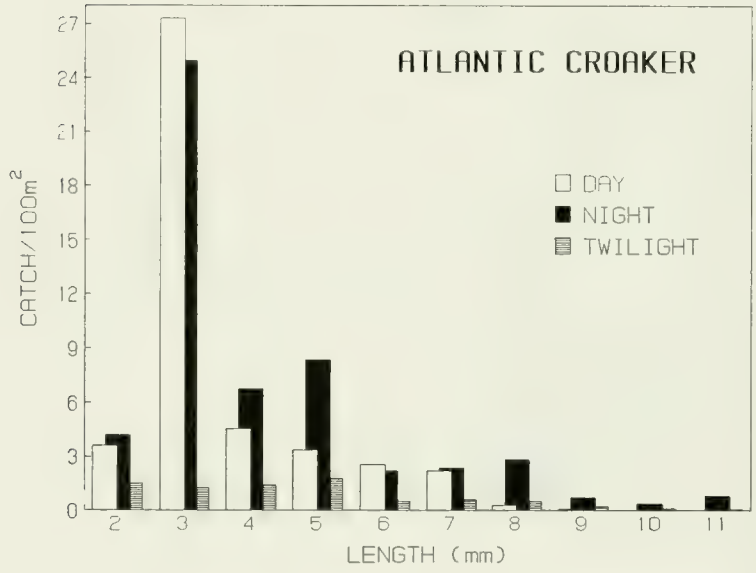
FIGURE 4.—*Continued.*


HADDOCK
DAY
NIGHT
TWILIGHT
CATCH/100m²
LENGTH (mm)


OFFSHORE HAKE
DAY
NIGHT
TWILIGHT
CATCH/100m²
LENGTH (mm)


SILVER HAKE
DAY
NIGHT
TWILIGHT
CATCH/100m²
LENGTH (mm)





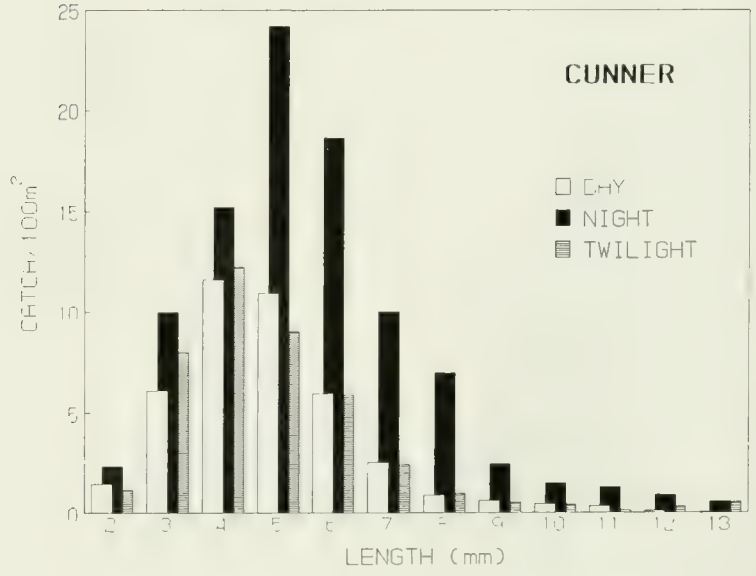
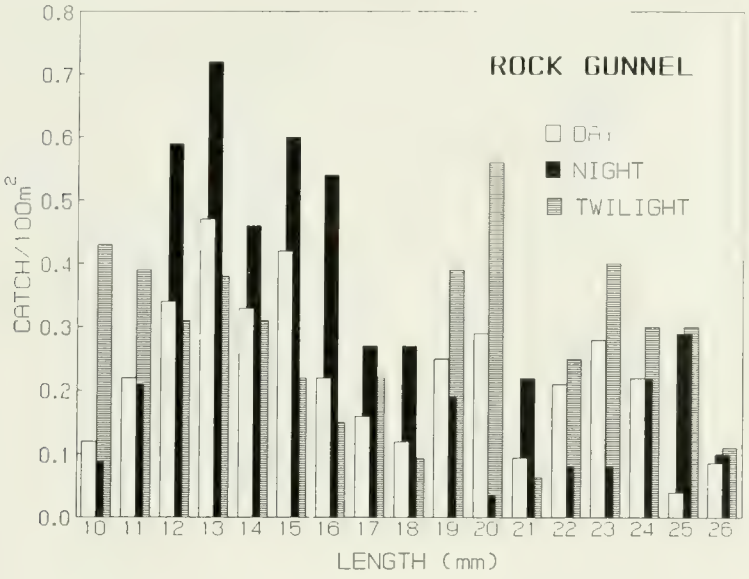
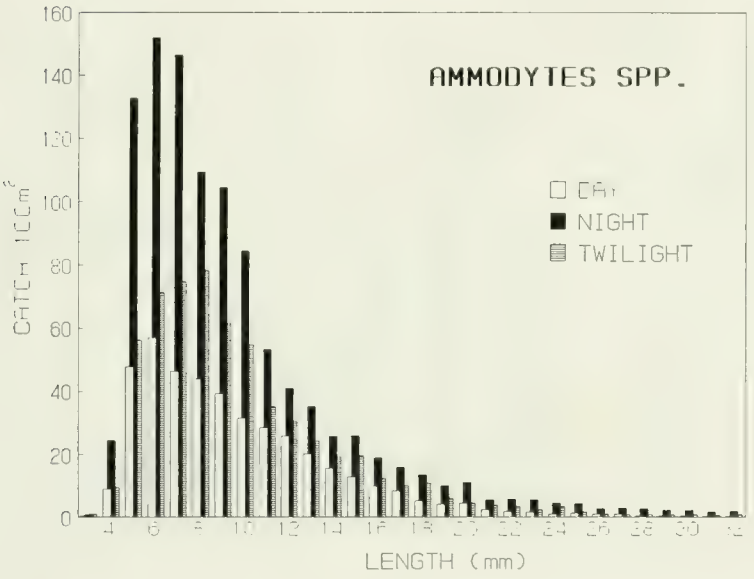
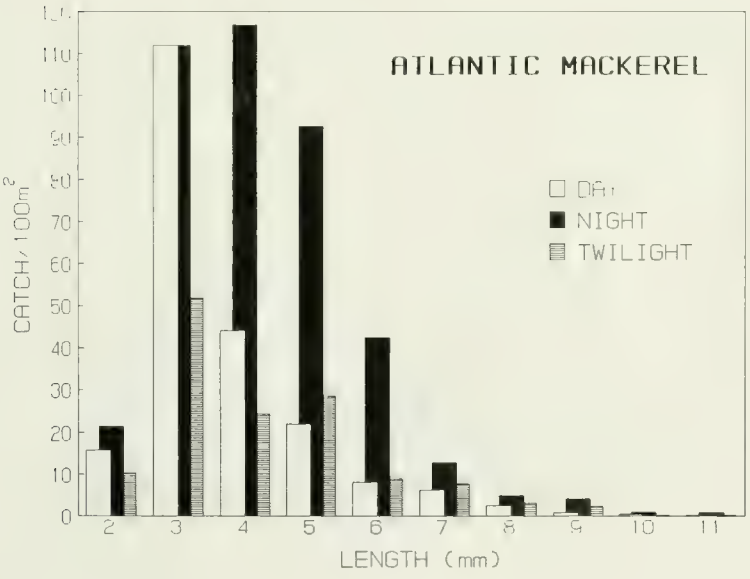
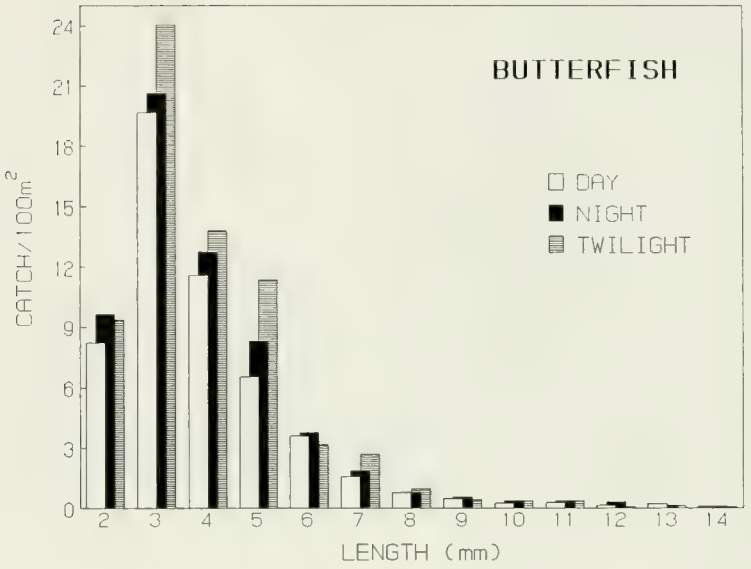


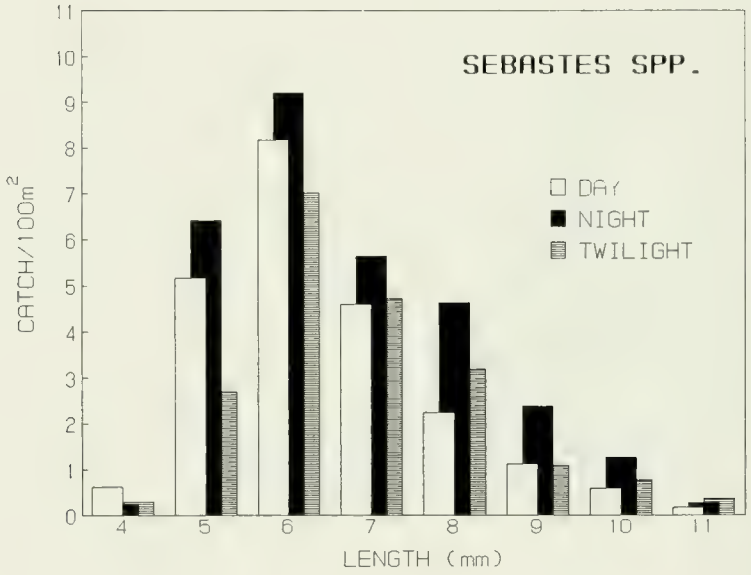
FIGURE 4.—*Continued.*


ROCK GUNNEL
DAY
NIGHT
TWILIGHT
CATCH/100m²
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26
LENGTH (mm)


AMMODYTES SPP.
DAY
NIGHT
TWILIGHT
0
20
40
60
80
100
120
140
160
LENGTH (mm)


ATLANTIC MACKEREL
DAY
NIGHT
TWILIGHT
CATCH/100m²
0
10
20
30
40
50
60
70
80
90
100
110
2 3 4 5 6 7 8 9 10 11
LENGTH (mm)





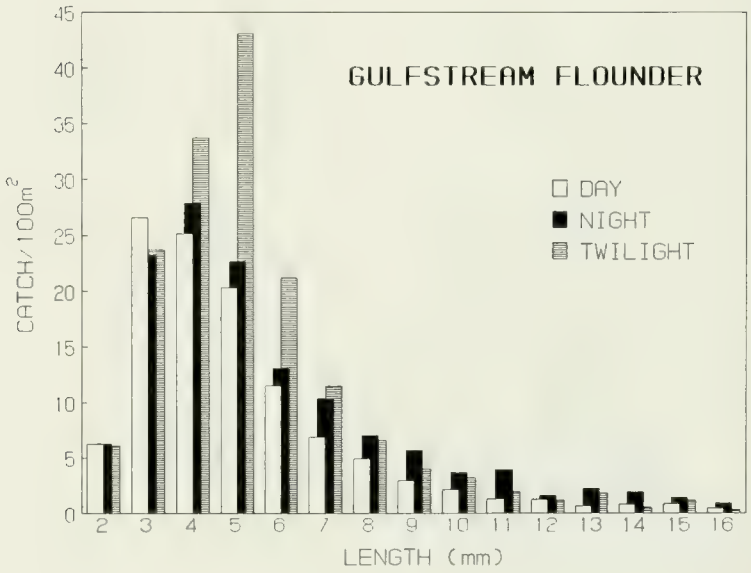
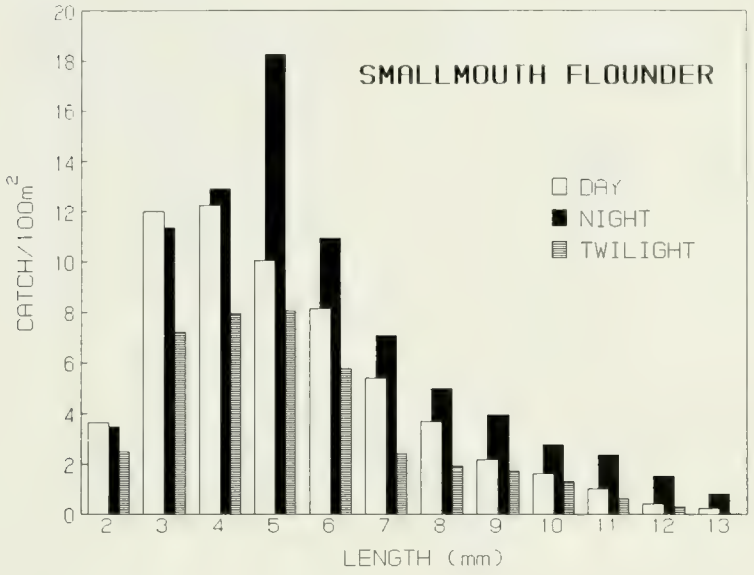
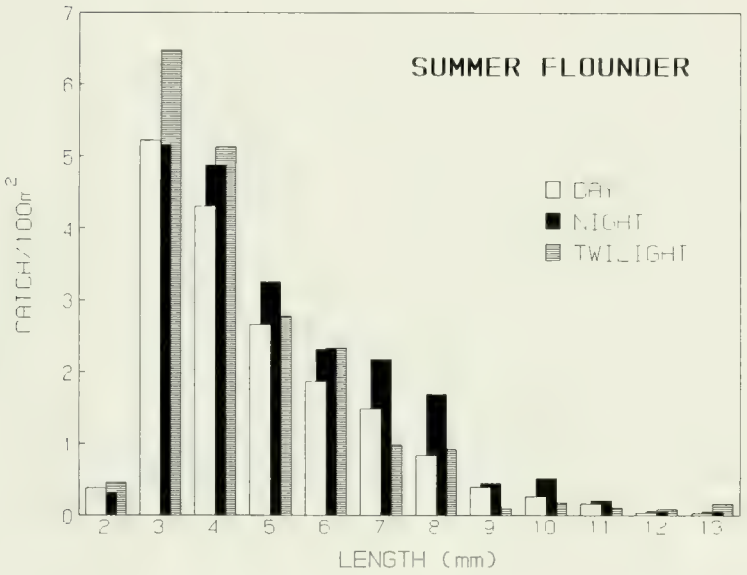
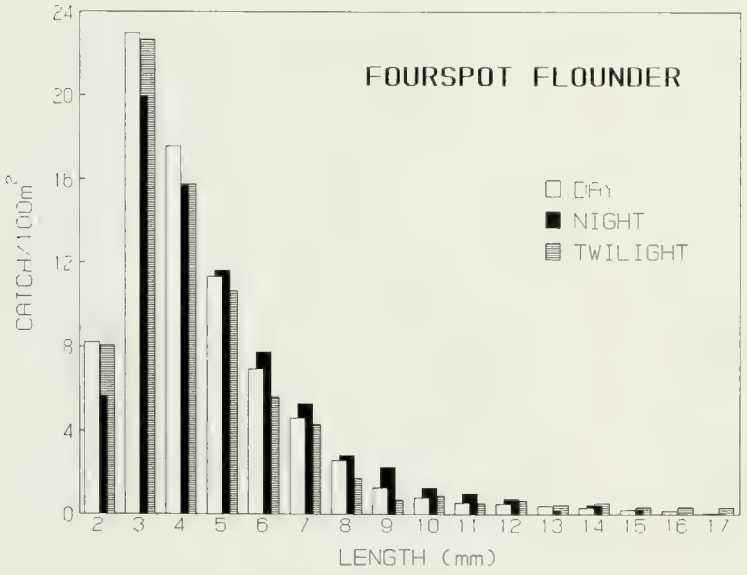
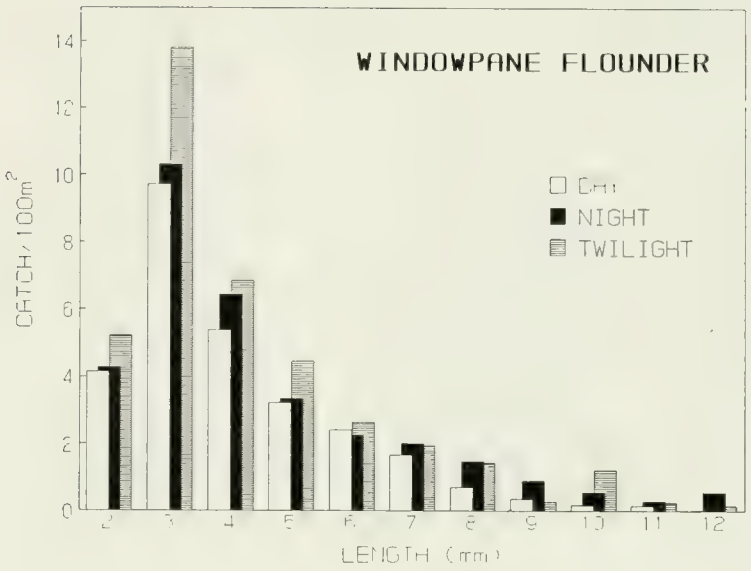


FIGURE 4.—*Continued.*


SMALLMOUTH FLOUNDER
DAY
NIGHT
TWILIGHT
CATCH/100m²
LENGTH (mm)


SUMMER FLOUNDER
DAY
NIGHT
TWILIGHT
CATCH/100m²
LENGTH (mm)


FOURSPOT FLOUNDER
DAY
NIGHT
TWILIGHT
CATCH/100m²
LENGTH (mm)



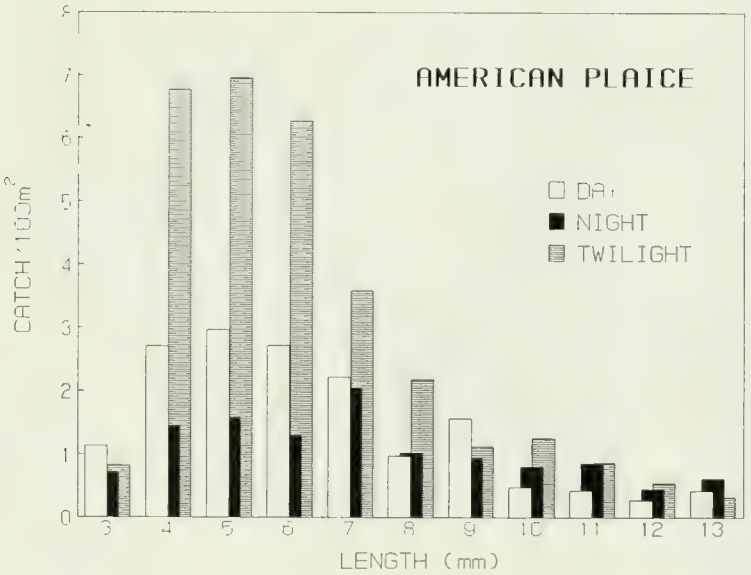
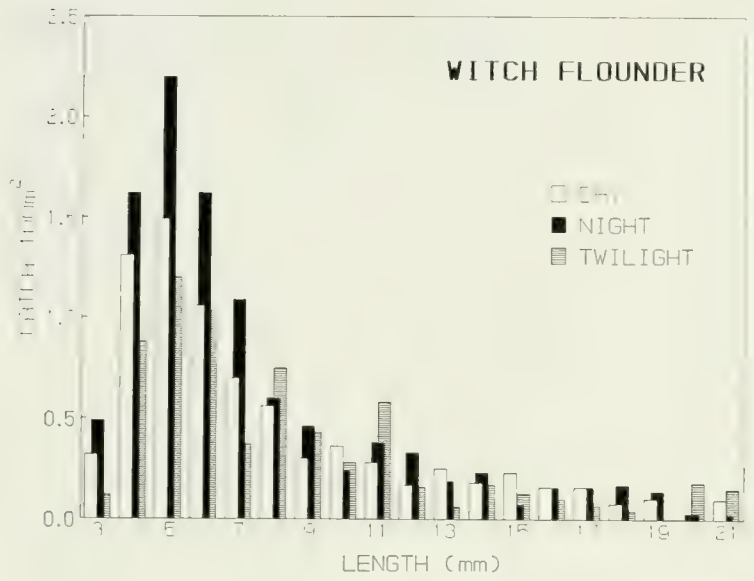
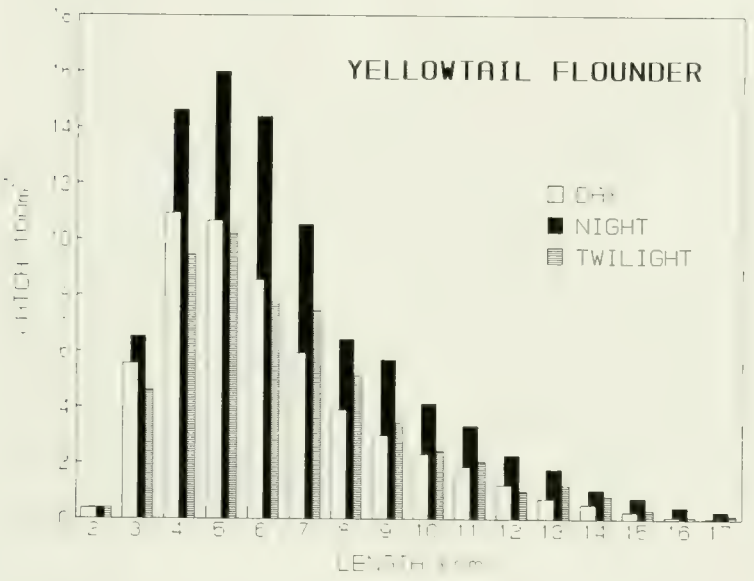


FIGURE 4.—*Continued.*

the haddock. Both butterfish and *B. glaciale* catches are about the same for night and day, regardless of length. Three species show a trend of decreasing ratios of night:day with increasing length with night catches exceeding day catches at the smaller lengths: witch flounder, *Glyptocephalus cynoglossus*; fourspot flounder, *Paralichthys oblongus*; and fourbeard rockling, *Enchelyopus cimbrius*. The last three species, Atlantic cod, *Gadus morhua*; goosefish; and American plaice, *Hippoglossoides platessoides*, have day catches exceeding night catches at the small lengths and as they grow the ratios of night:day equal or exceed one.

If net avoidance by fish larvae is visually cued, the expected ratios of twilight-to-day catches would exceed one and increase with increasing fish length. Another expectation would be that night catches would exceed, on average, twilight catches. As shown in Table 3, 16 of 36 taxa conform to the ranking of night > twilight > day catches. A total of 16 of the 26 taxa analyzed by length (Fig. 4) shows increasing twilight:day catch ratios, determined from expected values from the regression analysis, with increasing length. However, Figure 4 also shows twilight catches often exceeding night catches at some lengths for many taxa. Outstanding examples of dominant twilight catches are offshore hake, American plaice, butterfish, and windowpane flounder, *Scophthalmus aquosus*. The catches of offshore hake show that twilight catches domi-





nate at all lengths (≈ 50% of the total catch) and day catches amount approximately to only 20% of the total. This relationship of catches is unique among the 26 taxa analyzed and is statistically significant ($P < 0.01$, Table 3). Offshore hake larvae occur mostly at the shelf break in depths > 200 m (Morse et al. 1987). Since the maximum water column depth sampled by the net was 200 m, collections of this species may reflect a vertical migration pattern into the net sampling area during twilight as well as visually cued net avoidance.

The catches of *B. glaciale*, *C. maderensis*, Atlantic herring, and rock gunnel, *Pholis gunnelus*, reveal some unique characteristics as analyzed by day, night, and twilight. The length range for *B. glaciale* in Figure 4 is 3–11 mm, but the entire range sampled during this study is from 3 to 52 mm. At 12 mm, the length at which metamorphosis occurs (Halliday 1970), this species is virtually absent from all daylight catches (i.e., 3 individuals > 11 mm in 2,201 tows) though they are abundant, measuring up to about 25 mm long, in both night and twilight tows. Larvae are most abundant at the offshore extreme of the survey area (Morse et al. 1987), and the average bottom depth where they occur is about 400 m while the maximum tow depth is 200 m. Assuming fish begin at metamorphosis, the characteristic vertical migrations of juveniles and adults, this extreme case of net avoidance represents the effect of vertical migration

during the day below the path of the net. Halliday (1970) found the center of distribution during the day is below 450 m (250 fathoms) and at night between 45 and 90 m (25 and 50 fathoms). In contrast to *B. glaciale*, the lanternfish, *C. maderensis*, was captured in all light regimes up to 16 mm. With this species, night catches dominated both day and twilight catches by up to 10 times, but the total length range captured changed little, regardless of light conditions. The length frequencies of Atlantic herring show a distinct polymodality for both day and night catches with peaks occurring at various lengths, depending upon the light regime considered (Fig. 4).

The catches of rock gunnel larvae are the most erratic of the 26 species presented. There appears to be little decrease in abundance with increasing length and they have the lowest ratios of day, night, and twilight catches of any taxa. Figure 4 shows a slight dominance of night catches at the smaller sizes and of twilight catches at the larger sizes. The minimum length (10 mm) corresponds to the large hatching size of rock gunnel and is the largest of any taxa treated here.

Correction Factors

The estimates of the coefficients of the expon-

TABLE 4.—Regression coefficients and mean square error (MSE) for the relationship of mean catch per 100 m^2 United States, 1977–84. Regression constants for the quadratic equation relating the ratios (R) of night:day and the estimate.

	Day			Night			Twilight		
Taxon	*a*	*b*	MSE	*a*	*b*	MSE	*a*	*b*	MSE
Atlantic herring	4.318 (0.478)	−0.290 (0.0293)	0.415	4.306 (0.241)	−0.186 (0.0147)	0.106	5.606 (0.623)	−0.323 (0.0381)	0.703
Ceratoscopelus maderensis	3.150 (0.484)	−0.400 (0.0423)	0.197	4.595 (0.321)	−0.338 (0.0280)	0.086	5.215 (1.043)	−0.504 (0.0912)	0.914
Benthosema glaciale	3.691 (0.334)	−0.404 (0.0405)	0.046	3.790 (0.507)	−0.422 (0.0615)	0.106	2.281 (0.654)	−0.204 (0.0794)	0.176
Goosefish	2.225 (0.308)	−0.383 (0.0323)	0.115	1.769 (0.514)	−0.348 (0.0539)	0.320	1.268 (0.573)	−0.299 (0.0600)	0.396
Urophycis spp.	4.602 (0.383)	−0.410 (0.0334)	0.379	4.828 (0.355)	−0.371 (0.0310)	0.326	4.488 (0.394)	−0.321 (0.0344)	0.402
Fourbeard rockling	2.809 (0.332)	−0.600 (0.0445)	0.119	2.688 (0.181)	−0.550 (0.0243)	0.035	1.193 (0.622)	−0.310 (0.0834)	0.417
Atlantic cod	3.185 (0.118)	−0.307 (0.0091)	0.034	2.423 (0.212)	−0.233 (0.0163)	0.109	1.972 (0.291)	−0.223 (0.0225)	0.206
Haddock	4.887 (0.339)	−0.442 (0.0336)	0.161	5.237 (0.458)	−0.546 (0.0453)	0.293	4.354 (0.333)	−0.418 (0.0329)	0.155
Offshore hake	3.521 (0.531)	−0.653 (0.0770)	0.249	3.384 (0.435)	−0.568 (0.0631)	0.167	4.432 (0.484)	−0.616 (0.0702)	0.207
Silver hake	4.560 (0.217)	−0.357 (0.0151)	0.176	4.195 (0.148)	−0.242 (0.0103)	0.082	4.043 (0.280)	−0.276 (0.0196)	0.294
Bluefish	7.453 (0.412)	−0.947 (0.0526)	0.116	6.260 (0.536)	−0.588 (0.0683)	0.196	6.406 (0.890)	−0.770 (0.113)	0.540
Atlantic croaker	5.974 (0.622)	−0.913 (0.0834)	0.417	4.065 (0.505)	−0.445 (0.0677)	0.275	1.891 (0.379)	−0.379 (0.0508)	0.155
Cunner	5.586 (0.385)	−0.655 (0.0411)	0.101	5.721 (0.279)	−0.497 (0.0298)	0.053	3.978 (0.923)	−0.449 (0.0990)	0.584
Rock gunnel	0.414 (0.707)	−0.106 (0.0355)	0.286	1.072 (0.912)	−0.133 (0.0458)	0.477	−0.253 (1.051)	−0.0712 (0.0527)	0.633
Ammodytes spp.	5.710 (0.104)	−0.223 (0.0050)	0.045	5.926 (0.117)	−0.177 (0.0056)	0.056	5.775 (0.141)	−0.203 (0.0067)	0.081
Atlantic mackerel	7.019 (0.181)	−0.782 (0.0243)	0.035	7.484 (0.432)	−0.701 (0.0579)	0.201	6.583 (0.651)	−0.732 (0.0873)	0.457

ential regression equations fitted to the mean catch per 100 m^2 and to the length for each taxa are shown in Table 4. The regression fitted to twilight catches is often not as accurate as for day or night. This is not surprising because twilight catches represent the transitional time between light and dark regimes when visual avoidance responses to the net are expected to be most variable. This variability is evident in the often high twilight catches at the larger sizes.

The ratios of expected catches calculated from the exponential regressions for night:day and twilight:day catches were fit to polynomial equations and yield corrections for catchability for day, night, and twilight catches (Table 4).

Mortality

Catches of each taxa were corrected for day, night, and twilight catchability, and the mean catch per tow (number/100 m^2) was again calculated for each mm length and the exponential decay model fit to the length frequencies. The slope of the fitted line was used as an estimate of length-dependent mortality (Ebert 1973). Mortalities ranged from 0.114 for rock gunnel to 0.701 for Atlantic mackerel (Table 5). A review of the spawning times of the 26 taxa (Colton et al. 1979; Morse et al. 1987) reveals that 4 of the 6 taxa with the lowest mortalities are winter spawners, and 5 of the 6 taxa with the highest

(C) versus larval length (mm) as $C = a * \exp(\text{length} * b)$ for day, night, and twilight by taxon for larvae caught off the northeast twilight:day mean catches verses larval length (L) where $R = a + b_1 L + b_2 L^2$. Numbers in parenthesis are standard error of

	N/D ratios			T/D ratios		
Taxon	a	b_1	b_2	a	b_1	b_2
Atlantic herring	3.101 (0.260)	−0.325 (0.0360)	0.0287 (0.00115)	3.580 (0.00341)	−0.109 (4.72×10^{-4})	0.00118 (1.51×10^{-5})
Caratoscopelus maderensis	4.572 (0.0372)	0.168 (0.00714)	0.0164 (3.22×10^{-4})	7.146 (0.0530)	−0.576 (0.0102)	0.0140 (4.49×10^{-4})
Benthosema glaciale	1.104 (4.77×10^{-5})	−0.0200 (1.25×10^{-5})	1.59×10^{-4} (7.70×10^{-7})	0.777 (0.0815)	−0.145 (0.0213)	0.0249 (0.00132)
Goosefish	0.637 (0.0815)	0.0209 (0.0213)	5.31×10^{-4} (0.00132)	0.424 (4.45×10^{-4})	0.0173 (1.07×10^{-4})	0.00297 (5.86×10^{-6})
Urophycis spp.	1.266 (0.00204)	0.0437 (4.32×10^{-4})	0.00142 (2.02×10^{-5})	1.061 (0.0296)	0.0181 (0.00630)	0.00909 (2.94×10^{-4})
Fourbeard rockling	0.892 (0.00101)	0.0407 (3.15×10^{-4})	0.00153 (2.22×10^{-5})	1.369 (0.268)	−0.477 (0.0834)	0.0707 (0.00588)
Atlantic cod	0.546 (0.0118)	0.0106 (0.00217)	0.00320 (8.90×10^{-5})	0.380 (0.0126)	3.7×10^{-4} (0.00231)	0.00299 (9.47×10^{-5})
Haddock	1.336 (0.00839)	−0.113 (0.00192)	0.00293 (9.97×10^{-5})	0.588 (1.37×10^{-4})	0.0136 (3.13×10^{-5})	2.09×10^{-4} (1.63×10^{-6})
Offshore hake	0.901 (0.00521)	0.0585 (0.00174)	0.00554 (1.32×10^{-4})	2.491 (8.63×10^{-4})	0.0883 (2.87×10^{-4})	0.00213 (2.18×10^{-5})
Silver hake	1.571 (0.164)	−0.180 (0.0284)	0.0227 (0.00107)	0.765 (0.0292)	−0.00350 (0.00505)	0.00575 (1.90×10^{-4})
Bluefish	8.415 (1.744)	−3.021 (0.495)	0.332 (0.0327)	0.688 (0.0570)	−0.0769 (0.0162)	0.0216 (0.00107)
Atlantic croaker	12.443 (3.420)	−5.265 (1.064)	0.572 (0.0750)	3.331 (0.981)	−1.408 (0.305)	0.146 (0.0215)
Cunner	2.614 (0.217)	−0.314 (0.0509)	0.0610 (0.00280)	1.032 (0.133)	−0.232 (0.0313)	0.0288 (0.00172)
Rock gunnel	1.902 (0.00146)	−0.0472 (1.53×10^{-4})	4.17×10^{-4} (3.93×10^{-6})	0.557 (0.00289)	0.0114 (3.5×10^{-4})	6.35×10^{-4} (7.78×10^{-6})
Ammodytes spp.	1.474 (0.0270)	0.0146 (0.00306)	0.00351 (7.72×10^{-5})	1.080 (0.00130)	0.0204 (1.48×10^{-4})	3.71×10^{-4} (3.73×10^{-6})
Atlantic mackerel	1.648 (0.00987)	0.100 (0.00309)	0.00918 (2.16×10^{-4})	0.651 (7.47×10^{-4})	0.0298 (2.32×10^{-4})	0.00113 1.64×10^{-4})

TABLE 4.—*Continued*

Taxon	Day			Night			Twilight		
	a	*b*	MSE	*a*	*b*	MSE	*a*	*b*	MSE
Butterfish	4.061 (0.332)	−0.479 (0.0362)	0.188	4.226 (0.276)	−0.482 (0.0300)	0.129	4.694 (0.323)	−0.548 (0.0353)	0.178
Sebastes spp.	6.661 (0.363)	−0.738 (0.0418)	0.030	6.415 (0.886)	−0.651 (0.102)	0.183	5.733 (0.395)	−0.606 (0.0455)	0.036
Gulf Stream flounder	4.637 (0.232)	−0.332 (0.0217)	0.086	4.624 (0.168)	−0.274 (0.0157)	0.045	5.524 (0.311)	−0.387 (0.0291)	0.154
Smallmouth flounder	6.088 (0.923)	−0.620 (0.0930)	0.714	4.802 (0.246)	−0.386 (0.0248)	0.051	5.145 (0.610)	−0.555 (0.0615)	0.312
Summer flounder	3.624 (0.271)	−0.516 (0.0315)	0.109	3.655 (0.378)	−0.481 (0.0439)	0.212	3.279 (0.517)	−0.468 (0.0601)	0.398
Fourspot flounder	4.218 (0.175)	−0.396 (0.0161)	0.072	4.635 (0.266)	−0.440 (0.0244)	0.166	3.514 (0.347)	−0.311 (0.0320)	0.287
Windowpane flounder	4.361 (0.361)	−0.612 (0.0450)	0.167	3.212 (0.261)	−0.365 (0.0325)	0.087	3.864 (0.449)	−0.466 (0.0560)	0.258
American plaice	2.460 (0.355)	−0.282 (0.0395)	0.129	1.117 (0.238)	−0.129 (0.0266)	0.058	3.650 (0.216)	−0.356 (0.0240)	0.048
Witch flounder	0.636 (0.220)	−0.153 (0.0158)	0.102	1.497 (0.329)	−0.222 (0.0237)	0.229	0.423 (0.446)	−0.148 (0.0321)	0.421
Yellowtail flounder	4.841 (0.323)	−0.421 (0.0278)	0.141	4.656 (0.140)	−0.331 (0.0120)	0.026	4.557 (0.337)	−0.376 (0.0290)	0.153

TABLE 5.—A list by taxa of the mean surface water temperature (T) of larval fish samples, the instantaneous growth rate (G_W), the minimum length (L_n) and maximum length (L_m) used in the analysis, the days (t) between L_n and L_m, and the instantaneous length (Z_l) and daily (Z_t) mortality rates.

Taxon	T (°C)	G_w	L_n (mm)	L_m (mm)	t (d)	Z_l	Z_t
Atlantic herring	10.5	0.134	7	24	38.16	0.196	0.0873
C. maderensis	19.9	0.269	6	16	15.13	0.338	0.223
B. glaciale	12.4	0.161	5	11	20.32	0.161	0.0780
Goosefish	19.3	0.261	4	14	19.92	0.366	0.261
Urophycis spp.	20.0	0.271	3	18	27.44	0.330	0.180
Fourbeard rockling	15.6	0.207	4	11	26.05	0.399	0.123
Atlantic cod	5.8	0.0661	4	20	101.20	0.259	0.0409
Haddock	6.5	0.0762	4	15	72.17	0.442	0.0674
Offshore hake	16.4	0.219	3	10	22.83	0.616	0.189
Silver hake	17.0	0.227	3	23	37.24	0.242	0.130
Bluefish	23.3	0.318	4	11	13.20	0.588	0.312
Atlantic croaker	20.5	0.278	3	11	19.40	0.481	0.198
Cunner	20.7	0.281	3	13	14.11	0.497	0.282
Rock gunnel	4.4	0.0459	13	26	62.67	0.114	0.0236
Ammodytes spp.	4.6	0.0488	5	32	157.86	0.177	0.0303
Atlantic mackerel	14.4	0.190	3	11	28.38	0.701	0.198
Butterfish	21.6	0.294	3	14	21.74	0.503	0.255
Sebastes spp.	13.3	0.174	6	11	14.46	0.606	0.225
Gulf Stream flounder	23.2	0.317	5	16	15.23	0.298	0.215
Smallmouth flounder	24.5	0.335	4	13	14.60	0.393	0.242
Summer flounder	15.1	0.200	3	13	30.43	0.481	0.158
Fourspot flounder	21.6	0.294	3	17	24.49	0.359	0.205
Windowpane flounder	16.2	0.216	3	12	26.63	0.403	0.136
American plaice	8.6	0.132	4	13	37.06	0.326	0.0791
Witch flounder	10.0	0.127	5	20	45.30	0.185	0.0612
Yellowtail flounder	13.8	0.181	5	17	28.06	0.331	0.142

Taxon	N/D ratios			T/D ratios		
	a	b_1	b_2	a	b_1	b_2
Butterfish	1.174 (*.*)	−0.00383 (*.*)	6.10×10^{-6} (*.*)	1.847 (0.00378)	−0.116 (9.81×10^{-4})	0.00251 (5.68×10^{-5})
Sebastes spp.	0.868 (0.00959)	0.0376 (0.00232)	0.00619 (1.36×10^{-4})	0.603 (0.0251)	−0.0189 (0.00608)	0.0107 (3.56×10^{-4})
Gulf Stream flounder	1.025 (0.00547)	0.0438 (0.00119)	0.00300 (5.88×10^{-5})	2.394 (0.00367)	−0.120 (7.99×10^{-4})	0.00213 (3.94×10^{-5})
Smallmouth flounder	2.969 (0.460)	−0.771 (0.103)	0.0763 (0.00536)	0.410 (0.00265)	0.0182 (5.73×10^{-4})	0.00152 (2.99×10^{-5})
Summer flounder	1.035 (5.52×10^{-4})	0.0346 (1.52×10^{-4})	8.42×10^{-4} (9.34×10^{-6})	0.715 (0.00106)	0.0309 (2.93×10^{-4})	0.00119 (1.80×10^{-5})
Fourspot flounder	1.508 (0.00136)	−0.0623 (3.03×10^{-4})	9.47×10^{-4} (1.49×10^{-5})	0.562 (0.0119)	0.0164 (0.00264)	0.00429 (1.30×10^{-4})
Windowpane flounder	1.527 (0.266)	−0.452 (0.0778)	0.0688 (0.00511)	0.854 (0.471)	−0.0232 (0.0137)	0.0203 (9.03×10^{-4})
American plaice	0.479 (0.0363)	−0.0424 (0.00920)	0.0116 (5.35×10^{-4})	3.222 (0.00740)	−0.214 (0.00187)	0.00484 (1.09×10^{-4})
Witch flounder	2.256 (0.00962)	−0.130 (0.00161)	0.00235 (6.12×10^{-5})	0.808 (*.*)	0.00429 (*.*)	1.23×10^{-5} (*.*)
Yellowtail flounder	1.061 (0.0310)	0.00562 (0.00606)	0.00905 (2.72×10^{-4})	0.770 (0.00207)	0.0282 (4.04×10^{-4})	0.00121 (1.82×10^{-5})

mortalities are summer spawners. The relationship of spawning time and mortality was investigated by calculating the weighted mean surface temperature for each taxa and plotting it against mortality (Fig. 5). Two linear regression lines are fitted to the data points: one for all the data (n = 26); and another without haddock, *Sebastes* spp., offshore hake, and Atlantic mackerel,

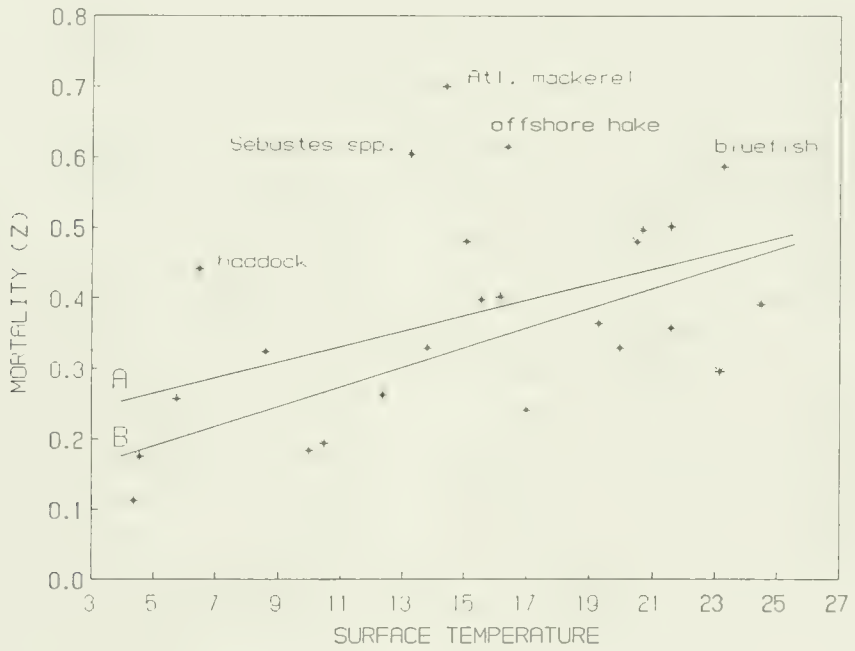


FIGURE 5.—Estimated length-dependent mortality versus mean surface water temperature for 26 larval fish taxa, 1977–84 (curve A, n = 26). Labeled points, except bluefish, were excluded from curve B, n = 22.

(those with the highest mortality (n = 22)). The correlations are significant for both data sets (P = 0.023 for n = 26 and P = 0.001 for n = 22) where r^2 = 0.20 and 0.51, respectively.

DISCUSSION

Net Avoidance

The correction of combined catches of all larvae presents a complex problem because of the interaction of the changes in catchability with the light regime, differential catchability with larval length, and the species composition of catches. The light regime and larval length appear to interact with the catches nonlinearly, as evidenced by the curvilinearity of the relationships of the ratios of night:day catches and larval length. The species composition of the catches represent an amalgam of the differing catchabilities of each taxa. This is illustrated in the catches by depth. Here the changing species composition with depth can be seen to change the ratios of day, night, and twilight catches. The correction for catchability on a station-by-station basis would require individual correction factors for each species in order to correct the entire survey catch. The correction factors presented here allow approximately 90% of all larvae, by numbers, to be corrected for light regime and larval-length catchability interactions.

Much has been written about net avoidance by fish larvae and the need to model length- and gear-dependent net avoidance (e.g., Clutter and Anraku 1968; Murphy and Clutter 1972; Barkley 1972; Ware and Lambert 1985). The models relate reaction distance, i.e., the distance between the net and larva when the net is first detected by the larva, larval swimming speeds, and net characteristics. The theories assume that, if a larva can detect the approaching net and produce sufficient swimming speed relative to net speed, it will avoid capture. This assumption seems unrealistic when compared with catchability using other types of gear. For example, if detection factors and swimming speed of fishes were applied to bottom trawls instead of plankton gear, it is clear that very few species of adult fishes would be captured. Catchability obviously involves numerous factors, and Barkley (1972) concluded that the application of net avoidance theory requires detailed knowledge of larval behavior, and net design and its fishing characteristics.

Corrections for day, night, and twilight catchability are not intended to account for all net avoidance by larvae. These corrections are intended to standardize the abundance of larvae from net catches, regardless of the light conditions. Obviously, net avoidance may and probably does occur (see Murphy and Clutter 1972), regardless of the light conditions, but before the application of theoretical corrections for net avoidance are attempted, it is appropriate to standardize the catches. Changes in catchability with varying light conditions and larval length are clearly demonstrated from this study. Many of the taxa show the expected relationship, if visual detection of the net is the primary cue for net avoidance, of night > twilight > day catches. Night:day catch ratios exceeding one are reported for a variety of gears and taxa (Alhstrom 1954; Bridger 1956; Richards and Kendall 1973; Lenarz 1973; Lough et al. 1982; Potter and Lough 1987; etc.). However, the dominance of twilight catches for Gulf Stream flounder, butterfish, American plaice, and offshore hake reveals a more complex nature for net avoidance and the need for species-specific studies as they relate to gear avoidance. It is difficult to speculate what behavioral mechanism is producing the increased twilight catches for these taxa, but perhaps light intensity within the water column and feeding behavior may be interacting to increase catchability of these larvae. A study of gut fullness and catchability, i.e., decreased mobility of larvae with full guts, could reveal a relationship between feeding, light intensity, and catchability.

Bimodal or polymodal length frequencies of Atlantic herring larvae appear common in field samples (e.g., Saila Lambert 1984 and Lough 1981), and are attributed to successive hatchings of larvae into the plankton community. It is unlikely that the combined-years' length frequencies in Figure 4 could reveal cohorts as described by Lambert (1984). A close look at the catches of larvae show day catches have just two or perhaps three modes and night catches have at least five modes while twilight catches have at most two modes. The combined length frequency of all larvae captured, regardless of hour of capture, is unimodal at 7 mm. At this point it is difficult to speculate on the causes of different polymodal length frequencies for day and night catches, but future studies of Atlantic herring larval abundance should be done cautiously when examining length-frequency curves.

Mortality and Growth

Survey timing has a profound effect on the mortality estimates from either length- or age-frequency curves. This is most evident if samples are not taken systematically during the spawning season and surveys are not timed and spaced evenly along the spawning curve (Hewitt and Methot 1982; Morse and Hauser 1985; Hauser et al. 1988). Mortality is overestimated from samples taken when spawning or larval production is increasing and underestimated when spawning is decreasing. The magnitude of the bias in mortality estimation shows a twofold to threefold decrease with samples from the beginning to the end of spawning. However, if survey samples are summed over the larval production cycle and at least four surveys are spaced evenly throughout the spawning cycle, the over- and underestimates cancel out and the combined data give a good estimate of mortality (Hewitt and Methot 1982). The process of combining surveys across years increases the number of samples taken during the spawning cycle from approximately 2 to 5 for each year to an observation every 4 to 10 days during the combined production cycle for each taxa. The result of this process is the calculation of an average length-dependant larval mortality for the eight years covered by this study.

The relationship of larval mortality and water temperature has some interesting implications about larval growth rates. Mortality, as an expression of the decrease in numbers over time by substituting time (t_i) for length (X_i) in Equation 2, is directly related to larval growth rate by the term t_i. The assumption is that, as fish larvae grow, mortality rate decreases (Ware 1975). With constant predation rates, the amount of time spent at a given size, commonly referred to as "stage duration", will determine the number of surviving larvae. The implication of this relationship of growth rate and mortality is that, owing as water temperature increases, stage duration will decrease to increased growth rate and the shorter stage duration will decrease mortality. This assumes that adequate food supplies are available for the increased metabolic demands of increased growth rates. The link between "stage duration" and particle-size dependent mortality rates would appear to be valid for most pelagic fish larvae given the rather small size range of newly hatched fishes. However, if larval mortality rates were, in fact, dependent upon growth rates as outlined above, fishes spawning in warm waters would derive a significant survival advantage over cold water spawners and mortality would be inversely correlated with growth rates.

According to population dynamics theory, mortality and growth rates must be positively correlated with the ratio of the instantaneous growth rate to instantaneous mortality rate, averaging > 1 for the biomass of a cohort of fish to increase (Beverton and Holt 1957; Ricker 1975; Ware 1975). If this were not the case, the maximum biomass of a cohort would occur at the egg stage. The results presented here (Fig. 5) show that length-dependent larval mortality is positively correlated with mean surface water temperature, and it seems clear that estimated mortalities are higher in the warm-water months than during winter. The association of temperature and larval growth rate was determined from a review of laboratory studies of larval growth rates (Table 6). The relationship of increasing growth rate with increasing temperature is not surprising, but the high coefficient of determination (93%) is surprising, given the variety of experimental procedures, prey species, densities, and fish species utilized by the experimenters. The data in Table 6 and the relationship of temperature to mortality confirm the positive correlation of growth and mortality.

Because expected ratios of instantaneous growth and mortality rates have been shown to be temperature-dependent, either rate is easily determined if the other is known. This ability to calculate either rate would have direct applications in modeling larval fish populations as it relates to survivorship, predator-prey dynamics, and the expected effect of environmental temperatures. For this study, if growth rate is known, then the mortality rates from field samples could be investigated to determine if net avoidance is a serious bias as often speculated. Growth rates in weight in Table 6 are rates per day, but mortalities in Figure 5 are rates per mm length interval. To convert lengths to ages (t = days), the length (mm) to weight (μg), relationship and instantaneous growth rate are dimensioned in days and μg where

$$\text{Weight} = c * \text{Length}^b$$

and the instantaneous growth rate (G_n)

$$G_n = (\ln W_{i+1} - \ln W_i)/(t_{i+1} - t_i) .$$

Thus

TABLE 6.—Listing of instantaneous larval growth rates per day and water temperatures (°C) from laboratory growth studies and linear regression analysis.

Species	Temp.	Growth	Source
Atlantic cod,	4	0.0424	Laurence 1978
Gadus morhua	7	0.0762	Laurence 1978
	10	0.0916	Laurence 1978
Haddock,	4	0.0375	Laurence 1978
Melanogrammus	7	0.0569	Laurence 1978
aeglefinus	9	0.1434	Laurence 1978
	6	0.0408	Buckley et al. 1987
	6	0.0367	Buckley et al. 1987
Sand lance,	6	0.0877	Buckley et al. 1987
Ammodytes spp.	6	0.0845	Buckley et at. 1987
	8	0.1065	Buckley et al. 1987
Atlantic mackerel,	15	0.1755	Buckley et al. 1987
Scomber scombrus	15	0.1948	Buckley et al. 1987
Pacific mackerel,	19	0.3383	Hunter and Kimbrell 1980
Scomber japonicus			
Atlantic herring,	8	0.1165	Checkley 1984
Clupea harengus			
Winter flounder,	2	0.0263	Laurence 1975
Pseudopleuronectes	5	0.0598	Laurence 1975
americanus	8	0.1065	Laurence 1975
Walleye pollock,	9.3	0.1031	Bailey and Stehr 1986
Theragra chalcogramma			
Bay anchovy,	26	0.3439	Houde and Schekter 1981
Anchoa mitchilli			
Sea bream,	26	0.4050	Houde and Schekter 1981
Archosargus rhomboidalis			
Lined sole,	28	0.3257	Houde and Schekter 1981
Achirus lineatus			

Linear Regression Analysis of growth rate (Y) on temperature (X):
$Y = a + bX$ $a = -0.0174$ $b = 0.0144$ $S_{Y\,X} = 0.0314$ $r^2 = 0.928$.

$$t_{i+1} - t_i = b(\ln L_{i+1} - \ln L_i)/G_w .$$

Then Z_t, the instantaneous mortality rate per day, where $t_{i+1} - t_i$ equals one day, is calculated as

$$-Z_t = (\ln N_0 - \ln N_t)/t$$

based on

$$N_t = N_0 e^{-Zt}$$

where N_0 is number at L_0 and N_t, adjusted for stage duration, is number at L_t. G_w for each species was estimated from the growth rate – temperature relationship in Table 6. The length-weight exponent (b) was estimated as the mean regression coefficient for seven species in Laurence (1979) at 4.15 (SE = 0.14). G_w and Z_t were calculated for 26 taxa and are shown in Table 5. The equation relating mortality (Z_t) to temperature (T) is

$$Z_t = -0.2722 + 0.01015\ \mathrm{T}$$

$$r^2 = 0.80 \quad S_{Y.X} = 0.0380.$$

As mentioned above, the ratio of growth rate to mortality rate must exceed one and as Ware (1975) estimated from three data points, the ratio of mortality to growth is near 0.7. The slope of the linear regression for the species in Table 5 is 0.820. Five taxa are near or greater then a ratio of one (i.e., mortality ≥ growth): Atlantic mackerel, *Sebastes* spp., haddock, cunner, and bluefish (Fig. 6). The mortality rates calculated for these taxa are suspect and may represent excessive net avoidance by the larger larvae. When these taxa are eliminated from the data the slope is 0.760 (SE = 0.051, n = 22). The

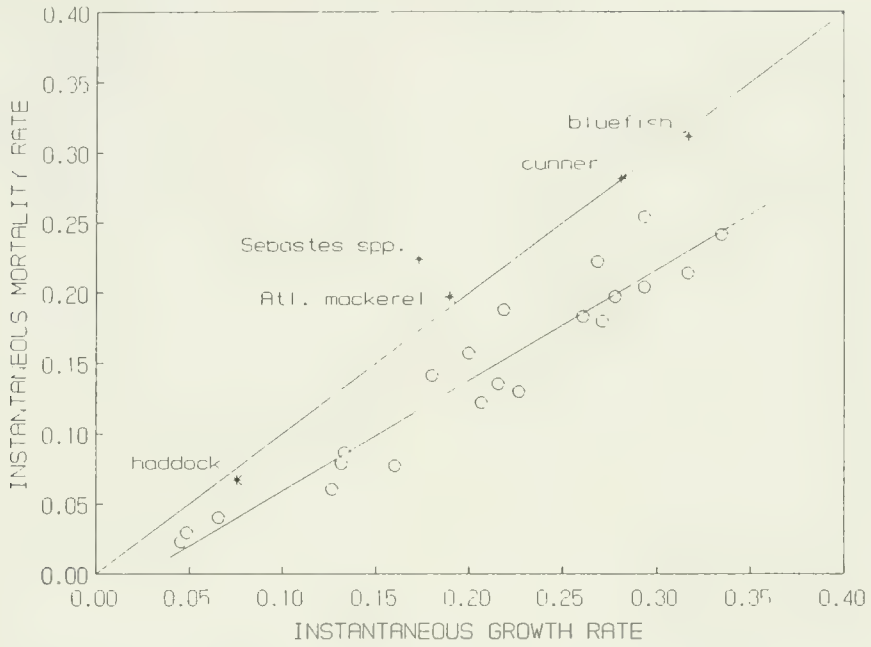


FIGURE 6—Plot of instantaneous larval mortality rates versus instantaneous growth rates for 26 larval fish taxa, 1977–84. Labeled points (n = 5) were excluded from the fitted curve.

ratios of mortality to growth coefficients for the rest of the taxa appear to be reasonable, i.e., approximately 0.7–0.8, and indicate that net avoidance is not a serious problem. It is interesting to note that the relationships of temperature- and length-dependent mortality (Fig. 5) showed that Atlantic mackerel, haddock, bluefish, and *Sebastes* spp. exhibit high mortality rates relative to the temperature, which lends support to the conclusion that net avoidance is the primary factor producing high mortality estimates. Offshore hake also shows a high mortality versus temperature, but does not exceed a ratio of one in the mortality versus growth rate plot. It is unclear which factor, temperature, net avoidance, mortality estimation, or a combination, is the dominant factor affecting the offshore hake data.

Contrary to this analysis, Houde (1989) found from a literature review of larval growth and mortality rates that mortality exceeded growth by about 40–100% over a temperature range of 5°–30°C. The relationship of growth to mortality during the larval stage has important implications about the life history dynamics during the first year of life. For example, when the expected growth and mortality rates at 10°C from Houde's study and this study are applied to 10^6 newly hatched larvae (weighing 0.05 mg each) until metamorphosis (38.2 mg), quite different results are found.

	Z_t	G_w	*Larval stage (d)*	*Metamorphosis*	
				No.	*Weight (g)*
This study	0.094	0.1266	59.09	3,799	145.12
Houde (1989)	0.1486	0.0904	80.11	7	0.26

The 3–4 orders of magnitude difference in numbers and weight at metamorphosis between the two studies indicate that the growth and mortality rates during the juvenile stage must be very different for recruitment to be successful. If the biomass of a year-class declines during the larval stage, as indicated by Houde (1989), then the ratio of growth to mortality must be high during the juvenile stage. Since growth rate tends to decline during the juvenile stage (Cushing 1975), compared to the larval stage, then mortality of the juvenile stage must be very low.

The close interdependence of larval growth and mortality rates on temperature is clearly demonstrated in this study. It is important to realize that these results represent average conditions for larvae during the eight years from 1977 to 1984. The average values for mortality, growth, and temperature form a baseline against which areal, seasonal, or annual variations in these important early life history parameters can be compared. Thus hypotheses about larval

growth or mortality can be quantitatively tested for significant deviations from the average expected values presented here. In addition, catchability of fish larvae by various plankton samplers can be compared with the expected mortality to determine serious biases.

The three major hypotheses suggested as mechanisms that control survival of larval fishes are starvation, predation, and advection into unfavorable environments. Clearly, advection is a special case which differs little from predation in its effects on the larval population and may be viewed as simply an abiotic "predator". The predator-prey interactions in the pelagic ecosystem may then be partitioned, in terms of mortality, into starvation and predation. It is often not clear whether larvae actually die from lack of adequate food supplies or become more vulnerable to predation as a result of starvation. In any case, larval mortality increases with increasing temperature, thus a major and consistent agent of mortality must be associated with water temperature. If the assumptions of size-dependent mortality, as explained by the "cube root rule", are valid, and there is no reason to reject them, predation rates on larvae must be the primary agent of mortality. Since metabolic rates increase with temperature ($Q_{10} \approx 2$–3; Hoar 1966), predator consumption rate would also increase. Thus increased growth due to increases in temperature would appear to impart no advantage to reduce larval mortality because of the concomitant increase in consumption rates of the predator field. Pauly's (1980) conclusions for juvenile and adult fishes support this hypothesis. An interesting consequence of this hypothesis is that, within the pelagic ecosystem, mortality rates will change with temperature without altering the predator field. Thus investigations of predator-prey interactions must account for the confounding effects of temperature on growth, consumption, and mortality.

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It is an honor to submit this contribution in dedication to Dr. Reuben Lasker, a pioneer in the study of early life history dynamics of fishes. His insight into the oceanic processes affecting larval fish survival has provided inspiration for this study.

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A Method for Correcting Catches of Fish Larvae For the Size Selection of Plankton Nets

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ABSTRACT: Length distributions of fish larvae obtained with plankton nets are usually biased because large larvae avoid the net and small larvae are extruded through the meshes. Such bias is often corrected by determining the ratio between a standard net and a test net with either zero extrusion or zero avoidance. However, when avoidance of the test net with zero extrusion or when extrusion through test net with zero avoidance differs from the standard net, then the usual method of correcting for size selection results in biased estimates. For such situations, we propose a method that explicitly considers both differential extrusion and differential avoidance and that provides estimates of variance for the corrected length-frequency distributions. The method was applied to length-frequency data for the Hawaiian anchovy or nehu, *Encrasicholina purpurea*. It was shown that a 1 m plankton net with 0.335 mm mesh dropped vertically through the water column during the day effectively samples nehu larvae only between 2.25 and 6.75 mm, roughly one-third of the total length range.

For many aspects of larval fish ecology, accurate estimates of length distribution are imperative, yet the length distribution of larvae obtained with a plankton net is nearly always biased because large larvae avoid the net and small larvae are extruded through the meshes. Previous research on methods to correct larval catches for such size selection has focused on either extrusion (Lenarz 1972) or avoidance (Barkley 1972; Murphy and Clutter 1972), implicitly assuming that the two aspects of size selection are independent. Although this assumption seems reasonable, situations arise in which the problems of estimating extrusion and avoidance are unavoidably linked.

Nearly all empirical or analytical studies of avoidance and extrusion are based on the premise that the number of larvae captured by a plankton net (N_o) is proportional to the number originally in the path of the net (N):

$$N_o = P_c\ N\ , \tag{1}$$

where the proportionality constant (P_c) varies with larval length. P_c can be considered as the probability of capturing a larva, and this, in turn, can be considered as a product of an entry probability (P_e) and a retention probability (P_r):

$$P_c = P_e\ P_r; \tag{2}$$

where P_e is equal to 1 minus the probability of a larva avoiding the net and P_r is equal to 1 minus the probability of a larva being extruded through the meshes, given that it has entered the net.

Since an estimator for N can be obtained by combining and rearranging the above equations,

$$N = \frac{N_o}{P_e\ P_r}\ , \tag{3}$$

the problem of correcting for size selectivity is one of estimating P_e and P_r for each length interval.

To estimate P_e or P_r, catches of a standard net are usually compared with those obtained by some test net used to sample the same population of larvae. In this paper, we will refer to these comparisons as either entry or retention experiments. Assuming catches are standardized to reflect equal filtration volumes, the general form of a net comparison is

$$\frac{N_{os}}{P_{es}\ P_{rs}} = \frac{N_{oi}}{P_{ei}\ P_{ri}} = N\ , \tag{4}$$

where the second subscript refers to the standard net (s) and to the test net used in either an entry experiment ($i = e$) or a retention experiment ($i = r$). Expressed in words, Equation (4) states that the corrected catches from the standard and test nets are both unbiased estimates of the true abundance of larvae and are therefore equal.

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For an entry experiment, an appropriate test net is one that has no larval avoidance (i.e., $P_{ee} = 1.0$) over the size range of interest. After substituting this value for the entry probability and rearranging terms, Equation (4) can be expressed as

$$\frac{N_{os}}{N_{oe}} = \frac{P_{rs}}{P_{re}} P_{es} . \quad (5)$$

Likewise, for a retention experiment, an appropriate test net is one that has no larval extrusion (i.e., $P_{rr} = 1.0$). After substituting this value for the retention probability and rearranging terms, Equation (4) can be expressed as

$$\frac{N_{os}}{N_{or}} = \frac{P_{es}}{P_{er}} P_{rs} . \quad (6)$$

To simplify Equations (5) and (6) further, previous studies have assumed that either the larval retention of the test net used in an entry experiment was identical to that of the standard net (i.e., $P_{rs} = P_{re}$; Barkley 1972; Murphy and Clutter 1972) or that the larval entry into the test net used in a retention experiment was identical to that of the standard net (i.e., $P_{es} = P_{er}$; Lenarz 1972; Colton et al. 1980; Leak and Houde 1987). With these assumptions, Equations (5) and (6) become

$$\frac{N_{os}}{N_{oe}} = P_{es} , \quad (7)$$

and

$$\frac{N_{os}}{N_{or}} = P_{rs} . \quad (8)$$

In other words, entry and retention probabilities of the standard net were estimated as the ratio of the catches of the standard and test nets within each length interval.

When neither assumption can be made, the estimation procedure is complicated in two ways: First, P_{es} and P_{rs} cannot be estimated as simple ratios of the catches of the standard and test nets because they additionally depend on other unknown entry and retention probabilities. This means that P_{es} and P_{rs} cannot be estimated independently for each length interval and must instead be expressed as functional relationships of larval length and estimated simultaneously for all size intervals. Second, the equations for the entry experiment, Equation (5), and the retention experiment, Equation (6), contain both P_{es} and P_{rs}; therefore, the two probabilities are confounded and must be estimated jointly.

In this paper, a method is described for estimating the entry and retention probabilities for this more difficult situation, and this method is then applied to correct the length-frequency distribution of larval Hawaiian anchovy or nehu, *Encrasicholina purpurea*, obtained with plankton nets.

MATERIALS AND METHODS

The standard plankton net that we used to sample eggs and larvae of nehu was constructed of 0.335 mm Nitex[1] and measured 1 m in diameter and 5 m long. The net was not towed but deployed instead by our allowing it to drop vertically through the water column until it hit the bottom, then retrieved with a line attached to a choke collar surrounding the mesh approximately 15 cm from the mouth of the net.

Retention and entry experiments were conducted on 28 March 1988 within Pearl Harbor, HI. The retention experiment consisted of 10 paired net drops, in which the standard net and a test net were deployed simultaneously at one location during daylight hours when the standard net was normally used. The test net was identical to the standard net in all dimensions, but it had a smaller mesh size (0.183 mm). The entry experiment was conducted at each of three nearby (<0.5 km distance) locations and consisted of five deployments of the standard net during the day and five deployments of the same net the following night at each location. Since sampling could not be paired in this experiment, we were concerned that patchiness and horizontal movement of fish by tidal currents might alter the length distribution between day and night sampling. To reduce this, the sampling locations chosen had weak tidal currents, and in addition, sampling was partitioned between three locations rather than concentrated at one. Water depth at all sampling locations was approximately 12 m. The sample obtained from each deployment of each net was stored separately in 10% buffered formalin.

During the retention experiment, the test net

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

appeared to become clogged with algae despite efforts to clean it between deployments. To determine whether the test net was indeed clogged and filtered less water than the standard net, we assumed filtration volume was proportional to the catch of nehu eggs and used a paired t-test to compare egg catches between nets. The test net caught significantly fewer eggs ($P < 0.05$); therefore, the test net was assumed to have filtered less water. To correct for the difference in filtration volume, larval catches in the test net were multiplied by the ratio of the egg catch of the standard net to that of the test net in each pair of deployments.

Nehu larvae were subsequently measured to the nearest 0.1 mm by using a video digitizing system (Optical Pattern Recognition System produced by Biosonics, Inc., Seattle, WA). For preflexion and early flexion larvae, length was measured from the snout to the end of the notochord. For larvae with fully formed tails, length was measured from the snout to the base of the caudal fin rays. The length distributions were not corrected for shrinkage due to preservation, but since all samples were maintained in preservative for about the same length of time, it is unlikely that shrinkage varied among samples.

The entry and retention probabilities were estimated by simultaneously fitting Equations (5) and (6) to the length-frequency data by using nonlinear regression, but before this could be done, three problems had to be solved. First, the entry and retention probabilities could not be estimated independently for each length interval; therefore, Equations (5) and (6) had to be modified so that the probabilities were expressed as functions of larval length. Retention probabilities were chosen to vary with length as logistic functions and thus have the form $P = 1/(1 + ae^{-bl})$, where a and b are parameters to be estimated and l is larval length (Ricker 1975). Entry probabilities, because they are decreasing functions of length, were chosen to have the form $P = 1 - (1/(1 + a\ e^{-bl}))$. After the logistic functions were substituted for the two entry probabilities (P_{es} and P_{er}) and two retention probabilities (P_{rs} and P_{re}) in Equations (5) and (6), the resulting statistical model had eight parameters.

Second, variability in the catch ratio changed with larval length, owing to the change in sample size, and necessitated the use of weighting factors in the regressions (Draper and Smith 1981). The weighting factors used were equal to $1/\text{var}(N_{os}/N_{oi})$, where *var* is the variance and N_{oi} can be either N_{or} or N_{oe}. Variance of the catch ratio was approximated by using the delta method (Seber 1973):

$$\text{var}(N_{os}/N_{oi}) = (1/N_{oi})^2\ \text{var}(N_{os}) + (N_{os}/N_{oi}^2)^2\ \text{var}(N_{oi}) - 2\ (N_{os}/N_{oi}^3)\ \text{cov}(N_{os},N_{oi}), \quad (9)$$

where cov indicates covariance. The number of larvae captured in each length class (N_o) was assumed to vary as a multinomial random variable. The variance of N_o was therefore expressed as $N_\bullet P(1 - P)$; where N_o is either N_{os}, N_{or} or N_{oe}; $N_\bullet$ is the sum of N_o over all length intervals; and $P = N_o/N_\bullet$. Although the covariance between the catches of the standard and test nets could be estimated for the retention experiment, it could not be estimated for the entry experiment because sampling was not conducted pairwise. However, the covariance term for the retention experiment was, for all size intervals, approximately 100 times less than the sum of the two variance terms (Equation (9)). On this basis, we assumed that the covariance term was generally small and could be ignored in both the entry and retention experiments.

Third, since the catch ratios fluctuated widely and often became infinite in the larger length intervals where sample sizes were small, the length distributions were truncated prior to fitting the equations. For the entry experiment, truncation occurred at the smallest length interval with zero catch by the test net. For the retention experiment, however, this rule resulted in an extremely narrow length range because the catches obtained with the test net were zero at relatively small lengths. To circumvent this problem, the inverse of Equation (5) was fit to the data, and truncation occurred at the smallest interval with zero catch by the standard net. Weights were calculated by using Equation (9) after substituting N_{os} for N_{oi} and vice versa.

Once Equations (5) and (6) had been fit to the data, the values P_{rs}, P_{re}, P_{es}, and P_{er} were estimated by evaluating the logistic functions at each 0.5 mm length interval using the parameter estimates. P_c for the standard net was calculated for each length interval as the product of the estimates of P_{es} and P_{rs}. Length-frequency data from nehu larvae were then corrected for extru-

sion and avoidance by dividing each N_o by the estimated value of P_c for the appropriate length interval. To better visualize the effect of this correction, we chose N_o from a data set that was considerably larger (N = 4,178) than those used in the net comparisons because histograms of this larger data set were smoother in appearance. This larger data set comprises all larvae that we have measured to date (including those obtained in the net comparisons) and that were collected during the day by the standard net.

The variance of the estimated value of N was approximated by using bootstrapping (Efron and Gong 1983): 1) each of the four experimental length-frequency data sets was randomly subsampled with replacement to produce four new samples with the same sample sizes as the originals; 2) Equations (5) and (6) were fit to the four synthetic samples by the methods described above; 3) P_{es}, P_{er}, P_{rs}, P_{re}, and P_c were estimated for each length interval; and 4) N for each length interval was estimated by dividing the N_o from the large sample of nehu length-frequency data by the estimated value of P_c. This procedure was repeated 500 times, generating 500 independent estimates of P_c for each length. To reduce variance owing to rare but extremely large estimates of N produced when P_c was near 0, the data were trimmed by eliminating the 25 largest estimates within each length interval (5% of the sample). After data trimming, the variance was calculated among the remaining 475 independent estimates.

The variances of P_{es}, P_{er}, P_{rs}, and P_{re} were also calculated from the same 500 independent estimates (no data trimming was required). A two-sample t-test incorporating these variances was then used to test for significant differences between P_{es} and P_{er} and between P_{rs} and P_{re} within each length interval.

RESULTS AND DISCUSSION

The estimated entry probabilities for the standard net (P_{es}) decreased from 1.00 for 3 mm larvae to near 0.00 for 10 mm larvae, whereas the entry probabilities for the small mesh net (P_{er}) decreased from 0.95 for 3 mm larvae to near 0.00 for 8 mm larvae (Fig. 1). When the apparent difference in entry probabilities between the two nets was examined statistically for each 0.5 mm length interval between 2.5 and 10.75 mm, P_{er} was found to be significantly less than P_{es} (two-sample, one-tailed t-test; $P < 0.05$) for all length

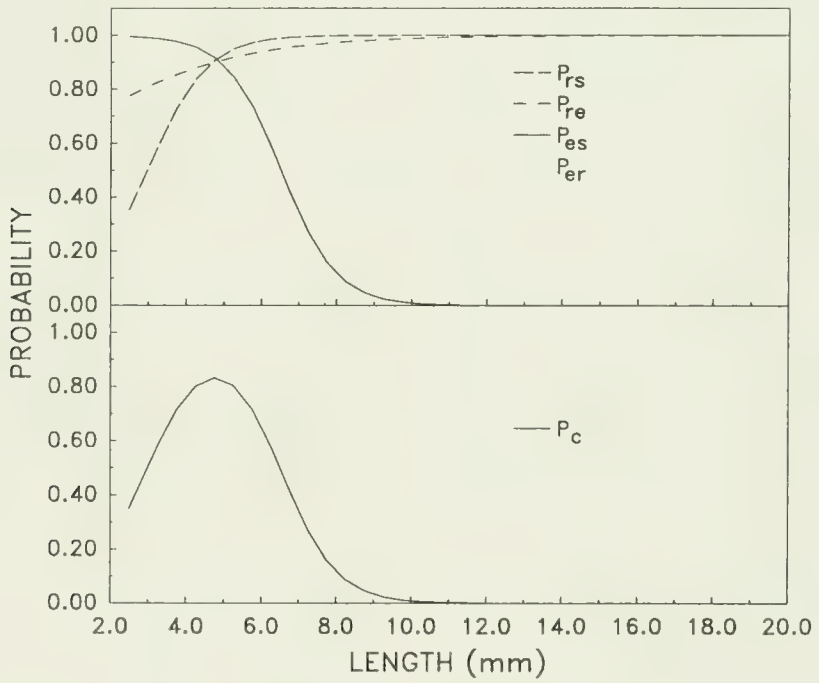

FIGURE 1.—Entry probabilities for the standard (P_{es}) and test nets (P_{er}) and retention probabilities for the standard (P_{rs}) and test nets (P_{re}) are shown by 0.5 mm length intervals (upper panel). Capture probability (P_c) for the standard net is shown by 0.5 mm length interval (lower panel).

intervals ≥4.25 and ≤6.75 mm. This result is surprising because the two nets were identical except for mesh size which, by itself, is unlikely to influence avoidance. However, the catch of nehu eggs in the test net was significantly less than in the standard net (paired t-test, $P < 0.05$), indicating, to the extent egg catches can be used as a measure of filtration volume, that the test net was likely clogged by abundant filamentous algae in Pearl Harbor during sampling. Such clogging not only decreased the apparent amount of water entering the test net but also may have slowed the sinking rate, allowing larvae to avoid the net more easily.

The estimated retention probabilities for the standard net (P_{rs}) during the day increased from about 0.35 for 2.5 mm larvae to nearly 1.00 for 6.0 mm larvae (Fig. 1). At night, however, the standard net appeared to have higher retention probabilities in the smallest length intervals (P_{re}; Fig. 1). When this difference was examined statistically (two-sample t-test), P_{re} and P_{rs} were not significantly different at $P \leq 0.05$ in any length interval, but they were significantly different at $P \leq 0.15$ within the two smallest length intervals. Although the differences between P_{re} and P_{rs} are relatively small, considering the same net and method of deployment were used during both day and night sampling, it is surprising that any differences were detected. One possible explanation is that the density of small larvae, rather than the retention probability, was higher at night. This could have occurred either because, by chance alone, the density of small larvae was higher in the patches sampled at night or because the mean density was higher as a result of eggs hatching between the day and night sampling. However, the addition of new larvae is unlikely because, at the time of year when our sampling occurred (March), nehu eggs hatch during the morning and new larvae would therefore have been equally available to both our day and night sampling (Clarke 1989). A second explanation is that the greater retention of small larvae at night is real and at least partially due to morphological changes increasing the catchability of larvae between the day and night sampling periods. Evidence for this is weak; however, Clarke (1989) reported that during March nehu larvae display considerable development of their eyes, mouth, and pectoral fins between midday and early evening of their third day of life. Development of such features might increase catchability relative to equal-sized, but undeveloped, larvae.

Regardless of the reasons, over some length ranges, $P_{rs} \neq P_{re}$ in the entry experiment and $P_{es} \neq P_{er}$ in the retention experiment; both cases are violations of the assumptions implicitly made when entry and retention probabilities are estimated as simple catch ratios (i.e., catch of standard net/catch of test net). The effect of ignoring this can be judged from plots of entry and retention probabilities estimated from simple catch ratios and estimates of P_{es} and P_{rs} using our method (Fig. 2). Entry probabilities estimated from simple catch ratios are similar to P_{es} for larvae ≥4.0 mm but are increasingly less than P_{es} at smaller lengths. This region of underestimation corresponds approximately to the length interval in which the retention of larvae differed between day and night (Fig. 1). Retention probabilities estimated from simple catch ratios are similar to P_{rs} at larval lengths <4 and >8 mm, but are considerably larger than P_{rs} at intermediate lengths. Again, this region of overestimation corresponds approximately to the length region in which avoidance differed between the standard and test nets (Fig. 1). Violation of the assumptions therefore leads to bias in estimates of entry and retention probabilities based on simple catch ratios.

The success of a net comparison, however, also depends upon the validity of several other assumptions. Foremost are the assumptions that no avoidance of the test net occurred in the entry experiment ($P_{ee} = 1.0$) and no extrusion through the test net occurred in the retention experiment ($P_{rr} = 1.0$). Violations of these assumptions lead to positive bias in the estimates of P_{es} and P_{rs}. For the entry experiment, P_{ee} was definitely higher than P_{es} over a broad range of sizes because more larvae were caught at night and a sizable fraction of the catch was larger than the largest larva caught during the day (Fig. 3). But no evidence indicates P_{ee} remained equal to 1.0 for size intervals ≤14.0 mm (the size of the largest larvae caught during the day), as is required to obtain unbiased estimates. For the retention experiment, P_{rr} was definitely higher than P_{rs} because more small larvae were captured with the test net (Fig. 3). But, again, no evidence indicates P_{rr} remained equal to 1.0 for size intervals ≥2.00 mm, the smallest size category.

Still another assumption is that, in each of the two experiments, the standard and test nets both sampled the same population of larvae. For the retention experiment, the assumption is certainly valid because the two nets were deployed

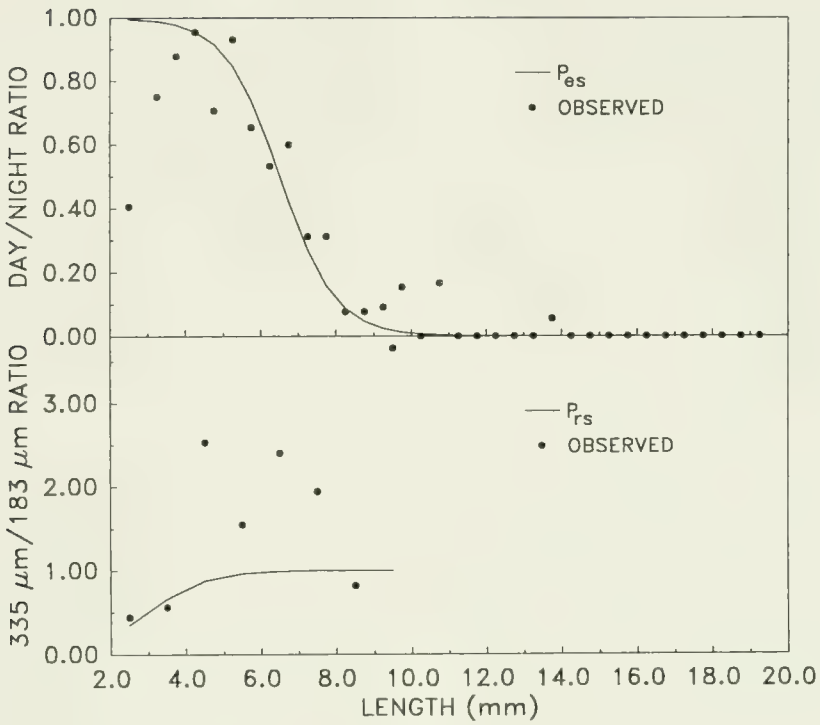

FIGURE 2.—Estimated values of P_{es} and the day to night catch ratio by 0.5 mm length intervals obtained in the avoidance experiment (upper panel). Estimates of P_{rs} and the 0.335 mm standard net to the 0.183 mm test net catch ratio by 1.0 mm length intervals obtained in the extrusion experiment (lower panel).

simultaneously from a small boat. For the entry experiment, however, deployment of one of the nets occurred approximately 10 hours after the other, and any patchiness in the larval distribution coupled with advective movement could have substantially altered the characteristics of the population sampled. We attempted to minimize this problem by increasing the sample size, relative to the retention experiment, and by partitioning the sampling among three locations rather than by concentrating it at one. Sampling variability, however, may still have been responsible for some of the differences between the day and night size distributions. This problem has been encountered in other studies using day and night comparisons to estimate entry probabilities (Murphy and Clutter 1972), and the only effective solution is increased sample sizes.

Since the method of estimating entry and retention probabilities proposed here requires more effort than that using simple catch ratios, it is important to determine at the outset whether the assumptions that $P_{rs} = P_{re}$ and $P_{es} = P_{er}$ have been violated so that the appropriate method of analysis can be chosen. Some indication of the validity of these assumptions can be obtained by examining plots of catch ratios as a function of larval length (Fig. 2). Two cases are evident in our data. First, if the assumptions are met, catch ratio should be a monotonically increasing or decreasing function of larval length because extrusion and avoidance are monotonic functions of larval length. This is not true in the avoidance experiment where the catch ratios increased for lengths $\leq$4 mm and decreased thereafter. Second, if the assumptions are met, catch ratios cannot be $>$1.0, because, except by chance alone, catch in the standard net is less than the catch in the test net. This is not true for the extrusion experiment where the catch ratios in some length intervals are $>$2.0. If either of these conditions are evident in plots of catch ratios, the method of estimating entry and retention probabilities proposed here is preferable to simple catch ratios.

Although we considered the problem in which both $P_{rs} \neq P_{re}$ and $P_{es} \neq P_{er}$, this is the most general of several related problems that could be approached with slight variations in our methodology. One example occurs when either $P_{rs} \neq P_{re}$ or $P_{es} \neq P_{er}$ but not both. In this case, either

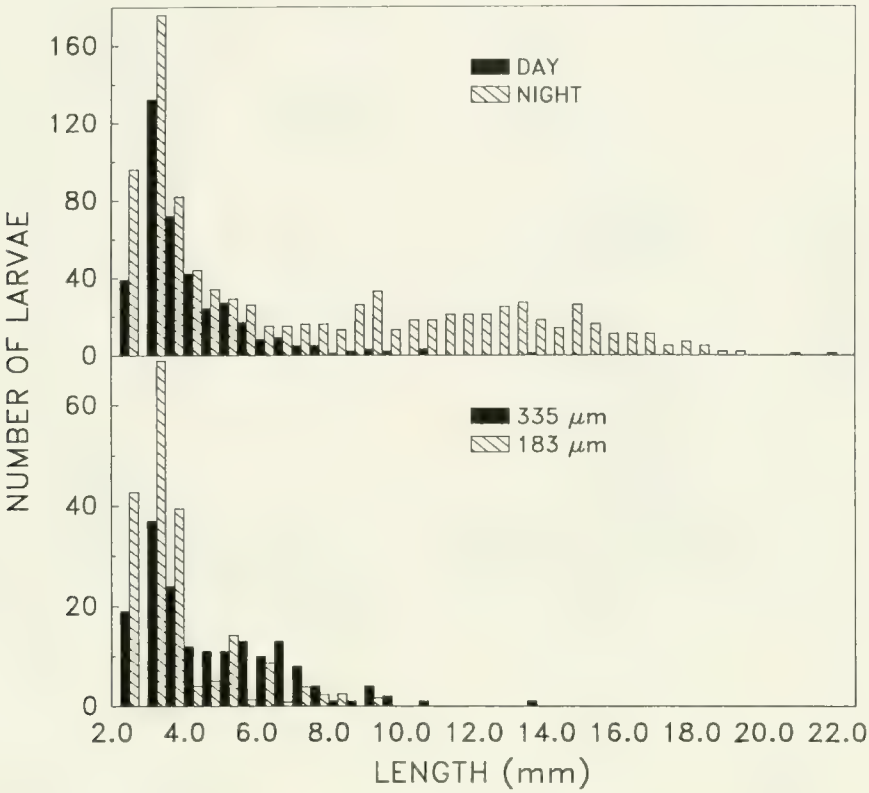

FIGURE 3.—The number of larvae by 0.5 mm length intervals captured in Pearl Harbor, HI, in March 1988. The entry experiment (upper panel) used a 0.335 mm standard mesh net during the day and night. The retention experiment (lower panel) used both a 0.183 mm mesh test net and a 0.335 mm standard mesh net during the day.

Equation (5) or (6) could be simplified by deleting either P_{rs}/P_{re} or P_{es}/P_{er}, but parameter estimation would still require a simultaneous fit of the two equations to the catch ratios. A second example occurs when only an entry experiment or retention experiment is conducted and the appropriate assumption is violated. In this case, the entry and retention probabilities still must be expressed as functions of larval length, thus requiring that nonlinear regression be used to fit either Equation (5) or (6) to the catch ratios.

The efficacy of the standard net at sampling nehu larvae can be judged in two ways. First, it can be judged by the length range sampled with a $P_c = 1.0$; that is, the range that requires no correction for extrusion and avoidance. For the standard net, P_c reaches a maximum of 0.86 at 4.25 mm and remains above 0.75 only over the interval 3.75–5.50 mm (Fig. 1). In other words, no interval within the larval length range of nehu (2.5–25.0 mm) is sampled completely with the standard net.

A second way of judging the efficacy of the standard net is by the length range than can be corrected, with sufficient precision, for extrusion and avoidance. The effect of correcting a large sample of nehu length frequencies for extrusion and avoidance can be seen in the frequency distributions before and after N_o was divided by the estimated value of P_c (Fig. 4). The precision of this correction can be gauged from the estimates of the variance of N (Fig. 5). Note that variance increases gradually with length until 6.75 mm and, thereafter, increases at a greatly accelerated rate. If 6.75 mm is chosen as the upper bound on the length interval within which the estimated numbers are considered sufficiently precise, then only one-third of the larval length range could be corrected to reflect the true length distribution. Thus, judging from either perspective, the standard net is a relatively ineffective tool for sampling nehu larvae.

Variance of the corrected length-frequency distribution was used above to define some length range that can be corrected for extrusion and avoidance with sufficient precision, but estimates of variance have other important uses,

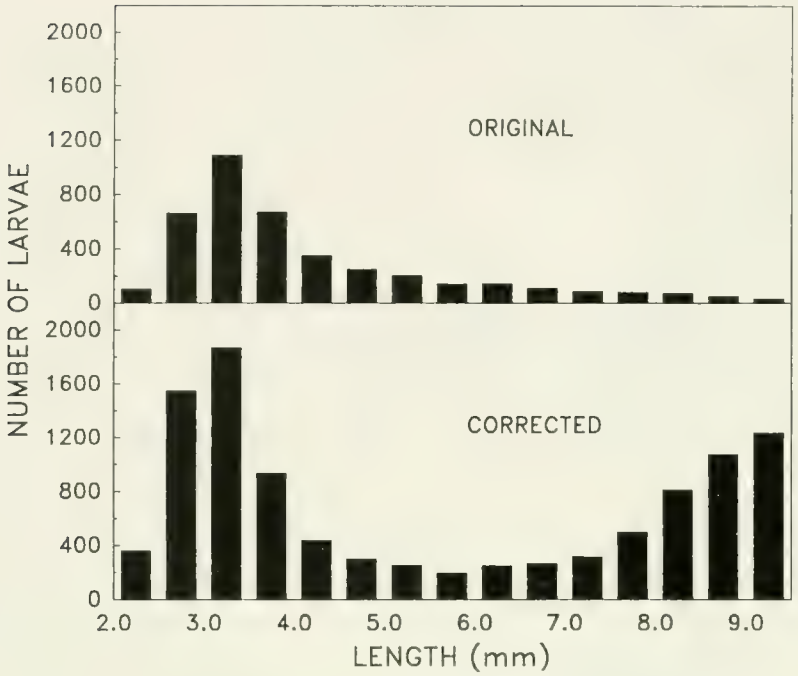

FIGURE 4.—Length distribution of nehu larvae by 0.5 mm intervals before correction for extrusion and avoidance (upper panel) and after correction (lower panel).

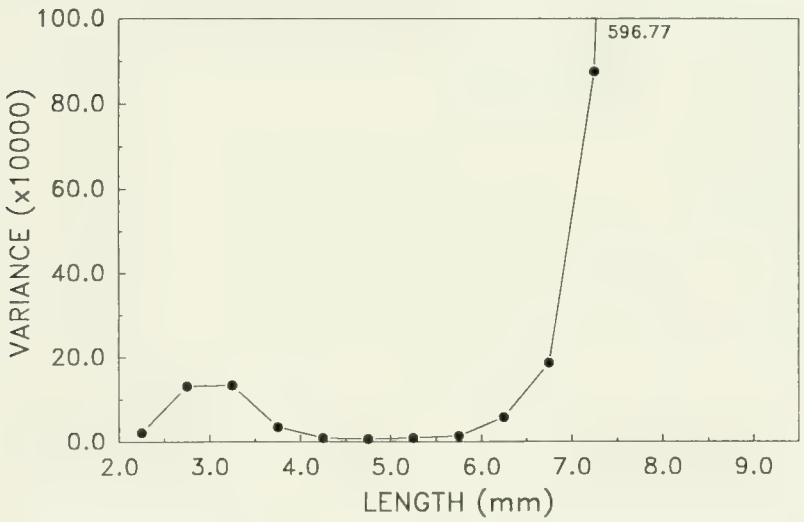

FIGURE 5.—Bootstrap estimate of variance of the corrected number of larvae by 0.5 mm length intervals.

especially when the corrected length-frequency distributions will be subsequently used to estimate mortality rates. Whether mortality is estimated by using methods that require converting length-frequency distributions to age-frequency distributions (Leak and Houde 1987) or by using some form of length-based method (Wetherall et al. 1987), precision of the mortality estimates will depend on the precision of corrected length-frequency distributions. Thus, procedures used to estimate mortality from larval length-frequency distributions should include weighting factors that incorporate the size-specific variances of the corrected length-frequency distributions.

Most of the problems associated with violations in the assumptions $P_{rs} = P_{re}$ and $P_{es} = P_{er}$ could be eliminated with proper attention to the

design of the entry and retention experiments. When these assumptions are violated, unbiased estimates of entry and retention probabilities can sometimes be obtained by restricting the analysis to either large or small larvae to ensure that avoidance and extrusion do not simultaneously influence the size distribution. If the size range of interest must be as broad as possible, however, then the methods described in this paper can be used to correct for differential extrusion and avoidance and unbiased length-frequency distributions can thereby be obtained.

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Midgut Cell Height Defines Nutritional Status of Laboratory Raised Larval Northern Anchovy, *Engraulis mordax*

Gail H. Theilacker and Yoshiro Watanabe

ABSTRACT: The height of the midgut mucosal cells was developed as a diagnostic index to assess the past feeding history of larval northern anchovy and to estimate starvation mortality of larval fishes in the sea. The index was compared to traditional histological indices and tested for field use. The height of the mucosal cells was a sensitive index, yielding reliable estimates of larval condition. Because it was sensitive, easy to measure and dependable in formalin-fixed tissue, this diagnostic index should be useful and practical for field work. Additionally, unlike other diagnostic criteria, it resisted the effects of autolysis (withstood prolonged time in the collecting net). Also included is a discussion of the growth characteristics of northern anchovy larvae that experienced a delay in feeding.

Larval mortality may determine recruitment of young fish to a fish stock. A major cause of larval mortality is starvation (Hunter 1976a; Lasker 1981). Several techniques have been recently developed to estimate the proportion of natural mortality caused by starvation. A histopathological technique that uses cellular criteria to identify larval nutritional condition was calibrated in the laboratory (O'Connell 1976; Theilacker 1978; Martin and Malloy 1980), applied to field studies to yield assessments of larval nutritional condition (O'Connell 1980; Theilacker 1986; Margulies 1986; Setzler-Hamilton et al. 1987), and successfully used to estimate rates of starvation-induced mortality (Theilacker 1986). Another technique that employs a morphometric approach generated good predictions of nutritional condition for several larval fish species (Theilacker 1978, 1986; Martin and Malloy 1980; Martin and Wright 1987; Setzler-Hamilton et al. 1987) as did the use of an RNA/DNA index (Buckley 1979; Wright and Martin 1985; Clemmesen 1987; Buckley and Lough 1987; Setzler-Hamilton et al. 1987).

Each of these diagnostic techniques suffers from various constraints. To develop histological criteria, an accurate representation of the structure of live tissue is needed for identifying larval fish condition. The usefulness of these criteria depends on the tissue quality of the field-collected specimens. For many fishes (northern anchovy and striped bass, *Morone saxatilis* (O'Connell 1980; Setzler-Hamilton et al. 1987)), autolytic tissue decomposition occurs within 2–3 minutes after sampling. Because routine ichthyoplankton collections usually take 21 minutes (Smith and Richardson 1977), special plankton collections are required for histopathology. Additionally the routine solution (3–5% formalin) used to preserve plankton does not adequately preserve cellular structure of larval fishes and special solutions (Bouin's fixative) must be used (O'Connell 1976; Theilacker 1978). The morphometric analysis requires extensive calibration studies to estimate the effect of the net and preservatives on shrinkage of body parts because the morphometric indices are very sensitive to shrinkage (Theilacker 1980; 1986). The RNA/DNA index must be calibrated for temperature effects and animal age (Ota and Landry 1984; Buckley 1984; Buckley and Lough 1987); however, there are other considerations that may limit its application. Furthermore, RNA/DNA is generally regarded as an index of potential growth (protein synthesis rates) not starvation mortality.

In March of 1985, we anticipated applying the histopathological technique developed by O'Connell (1976) to estimate starvation rates of northern anchovy collected at two sites off the coast of California (see Owen et al., 1989). However, when aboard ship, we found that it was impossible to preserve the larvae within the required 2–3 min time period (needed to maintain tissue quality) and take a sample that was representative of the zone inhabited by larval anchovy. We were unable to use the established histological criteria because it took us 5 or more minutes to sample larval anchovy from 50 m to the surface and process our collection. Thus, to estimate anchovy starvation rates, we needed to develop

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new criteria that were stable for a longer period.

Here we describe and evaluate a diagnostic index, the height of midgut mucosal cells of larval northern anchovy. The index is sensitive to feeding history, resistant to autolysis (withstands prolonged time in a collecting net), and simple to measure. It is reliable for fish fixed in formalin, the commonly used fixative for field collections.

METHODS

Experimental Design

We raised larval northern anchovy under different feeding conditions to produce specimens that exhibited various health states. These larvae were used to describe growth, determine the dominant midgut height measurement within each feeding treatment, evaluate the midgut index, and estimate response times. In a second series of experiments, groups of fed and starved fish were treated with nets in a manner designed to simulate plankton collection methods in the sea. These studies were used to evaluate how useful the new criterion would be in a field situation.

Rearing Treatments

Five groups of anchovy were raised at 15.5°C for three weeks in 100 L containers. The eggs, stocked at 10/L, were collected from a hormone-injected broodstock maintained at the Southwest Fisheries Center aquarium (Leong 1971). We fed the control group ad libitum on *Gymnodinium* and *Brachionus* (Lasker et al. 1970; Theilacker and McMaster 1971) at yolk absorption (four days after hatching at 15.5°C; hatching = day 0), and delayed feeding 1–4 days in the other groups. Fish were sampled daily from the fed, starved, and delay-fed treatments and preserved in Bouin's fixative (Table 1).

Field Simulation Experiments

One group of northern anchovy was fed for 3 days and one was starved for 3 days. We treated samples from each group of 7 d old fish in a net by flushing the submerged net with 15.5°C seawater for 0, 2, 5, 10, 15, 20, and 25 minutes (see Theilacker 1980 for details of this method). After the net treatment, fish were preserved in either 5% buffered formalin (standard shipboard fixative) or Bouin's solution (required fixative for histopathology).

Histological Preparation

We measured the standard length (SL) of preserved larvae to the nearest 0.01 mm and subsequently prepared them for histopathology using standard microtechniques (O'Connell 1976). Tissue was dehydrated, embedded in paraffin, serially sectioned at 6 μm in the sagittal plane, mounted, and stained with hematoxylin and eosin.

Measurement of Midgut Cell Height

The midgut is the major part of the intestine of

TABLE 1.—Standard length (SL) and

	Fed					
	Growth			Midgut		
Age (days)	*n*	SL[1] $\bar{x}$ mm	SD	*n*	SL[1] $\bar{x}$ mm	mght[2] $\bar{x}$ μm
4	FED					
5	32	3.95	0.23	10	3.93	19.63
6	34	3.92	0.21	17	3.87	20.13
7	26	4.33	0.24	13	4.29	19.52
8	33	4.59	0.46	19	4.67	19.13
9	33	5.29	0.40	10	5.26	22.13
10	38	5.54	0.33	10	5.85	21.88
11	26	6.22	0.47	10	6.09	21.13
12	55	6.36	0.48	10	6.52	20.75
13	38	6.85	0.43			
14	36	7.20	0.54			
17	66	7.22	0.74			
19	35	7.43	0.80			
Total *n*	452			99		

	Starved 3 d/fed					
	Growth			Midgut		
Age (days)	*n*	SL[1] $\bar{x}$ mm	mght[2] $\bar{x}$ SD	*n*	SL[1] $\bar{x}$ mm	mght[2] $\bar{x}$ μm
4	STARVED					
5	STARVED					
6	STARVED					
7	28	3.37	0.22	13	3.29	10.19
8	25	3.35	0.15	13	3.35	9.90
9	29	3.79	0.24	10	3.83	11.38
10	26	3.90	0.25	17	3.93	12.28
11	36	3.92	0.19	11	3.96	14.21
12	34	4.00	0.35	10	4.00	14.88
13	31	4.25	0.38			
14	26	4.63	0.41			
17	31	5.27	0.45			
19	30	5.51	0.68			
24	34	6.80	0.90			
Total *n*	330			74		

[1] SL taken on Bouin's fixed larvae
[2] Midgut cell height (see text)

larval northern anchovy; it extends from behind a constriction at the pylorus to another constriction at the beginning of the hindgut (Fig. 1). We measured the cell heights under a light microscope using the histological preparations. Epithelial cells of the midgut tend to decrease in height from the anterior part to the posterior end. We chose the midpart of the midgut (from 2/5 to 3/5 of the entire length) as the measurement site. The area is easily located in histological sections that are cut parallel to the median plane. The dorsal and ventral rows of midgut cells appeared in these sections. We measured the cells of the ventral row that were larger than the dorsal row, probably because of greater absorptive activity. We selected a section having four to six neighboring cells in which the nuclei, brush border, and cell base were clearly defined; brush border may be indistinct in larvae of poor condition. Measurements were taken from the luminal surface of the brush border to the cell base delimited by a basement membrane, using a micrometer attached to an eye lens. Usually, in sagittal sections, the cell heights are not so varied within the middle part of the midgut. If, however, there were slight differences between cells due to a slight angle of the section, we took an average of several measurements.

midgut cell height (mght) statistics for fed northern anchovy by diet and age.

	Starved 1 d/fed						Starved 2 d/fed					
	Growth			Midgut			Growth			Midgut		
Age (days)	*n*	SL[1] $\bar{x}$ mm	SD	*n*	SL[1] $\bar{x}$ mm	mght[2] $\bar{x}$ µm	*n*	SL[1] $\bar{x}$ mm	SD	*n*	SL[1] $\bar{x}$ mm	mght[2] $\bar{x}$ µm
4	STARVED						STARVED					
5	33	3.55	0.20	12	3.95	14.27	STARVED					
6	47	3.59	0.37	15	3.60	15.83	27	3.58	0.22	18	3.57	13.47
7	61	3.46	0.23	11	3.45	14.89	33	3.39	0.18	10	3.35	11.88
8	23	3.81	0.31	10	3.77	16.00	31	3.58	0.21	17	3.60	12.21
9	49	4.34	0.46	11	4.79	19.32	18	4.07	0.21	10	4.02	14.63
10	46	4.90	0.39	10	4.80	18.63	38	4.25	0.32	11	4.19	14.77
11	55	5.09	0.56				41	4.58	0.31	10	4.60	15.63
12	71	5.56	0.47				28	4.95	0.39			
13	47	5.86	0.45				27	4.99	0.41			
14	61	6.32	0.62				46	5.63	0.45			
17	121	6.84	0.86				33	6.25	0.73			
19	26	7.19	0.95				39	6.65	0.93			
Total *n*	640			69			361			76		

	Starved 4 d fed					
	Growth			Midgut		
Age (days)	*n*	SL[1] $\bar{x}$ mm	SD	*n*	SL[1] $\bar{x}$ mm	mght[2] $\bar{x}$ µm
4	STARVED					
5	STARVED					
6	STARVED					
7	STARVED					
8	19	3.40	0.19	10	3.44	10.51
9	14	3.58	0.22	6	3.59	10.00
10	6	3.66	0.12	6	3.66	8.13
11						
12						
13						
14						
17						
19						
24						
Total *n*	39			22		

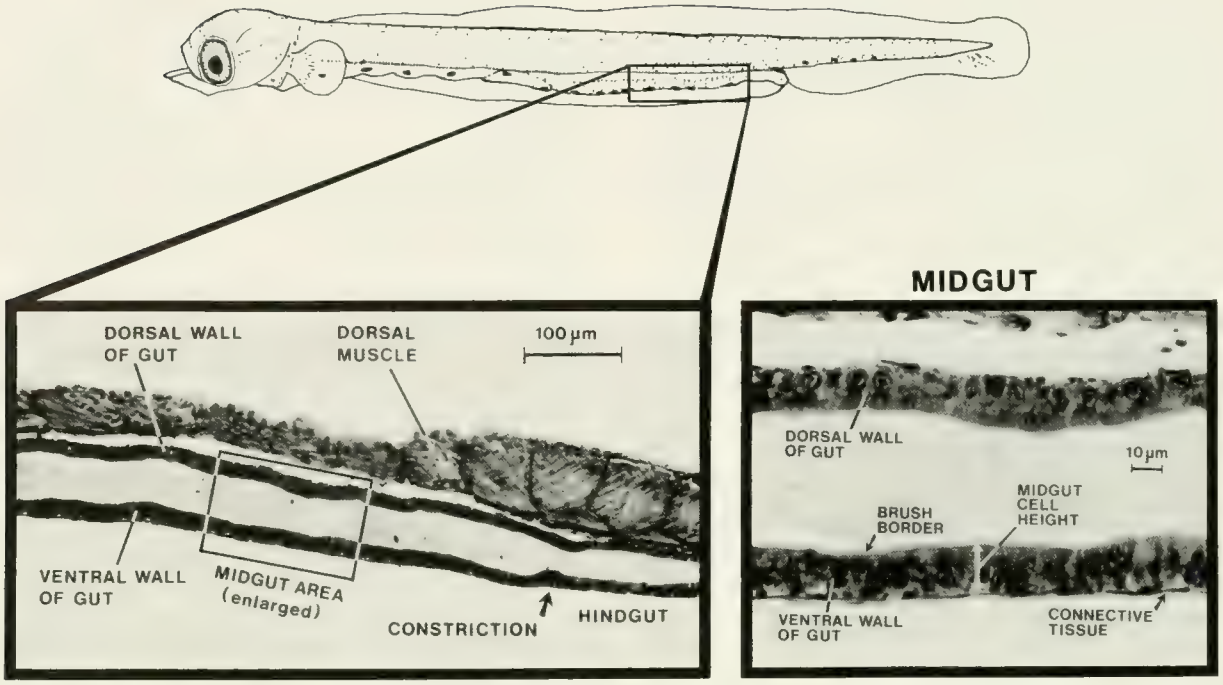

FIGURE 1.—*Engraulis mordax* larva showing measurement site for midgut cell height.

Evaluation of Midgut Criteria

To evaluate the capacity of the midgut cell height measurement to classify larval anchovy condition, we graded 5–10 larvae taken daily from 3 treatments (fed, feeding delayed 1 day, and starved) using both O'Connell's (1976) histological criteria and the midgut cell height. We assumed that the histological criteria (the sum of the cellular grades for the brain, cartilage, notochord, musculature, liver, and midgut) would yield the best estimate of larval condition, and we compared the power of each index to predict past feeding history.

RESULTS

Diet-Induced Differences in Growth

Growth of the fed control group was 0.41 mm/d, similar to published reports for northern anchovy raised in the laboratory (Kramer and Zweifel 1970; Hunter 1976b; Theilacker 1987). Larvae experiencing a feeding delay of 1, 2, and 3 days were smaller at 10.8 days than larvae not experiencing a delay, and as the starvation interval increased, their final size decreased (Table 2). For the test of significance of size at age, P was <0.01 for all delay combinations except the starved 3 d/fed (S3/F) vs. the 4 d delay in feeding

TABLE 2.—Diet-induced differences in growth of northern anchovy at a common age and at a common feeding period (n's for common feeding period slightly less than n's for common age).

		Common age			Common feeding period		
Diet	n	Age d	Feeding period d	SL $\bar{x}$ mm	Age d	Feeding period d	SL $\bar{x}$ mm
Fed	452	10.8	6.8	5.58	10	6	5.51
Starved							
1 d/fed	640	10.8	5.8	4.87	11	6	4.96
2 d/fed	394	10.8	4.8	4.48	12	6	4.75
3 d/fed	372	10.8	3.8	4.00	13	6	4.32
4 d/fed	114	10.8	2.8	3.98	—	—	—

(S4/F) where $P = 0.8$, indicating that delaying feeding affected the final fish size at a given age (ANOVA; Table 2).

Progressively increasing the periods of starvation before feeding also caused a decrement in the growth rate after feeding resumed (Fig. 2; Table 2). Larvae were unable to compensate for a delay in feeding at the onset, and fish length at an age where all fish had been feeding for 6 days differed for each treatment [$P = < 0.01$ for all diet combinations except starved 1 d/fed (S1/F) vs. 2 d delay in feeding (S2/F) where $P = 0.08$ (ANOVA; Table 2)]. Growth rates for the 6 d period ranged from 0.41 mm/d for the fed group, 0.39 mm/d for 1 d delay in feeding (S1/F), 0.34 mm/d for 2 d delay (S2/F), 0.31 mm/d for 3 d delay (S3/F). Length was transformed to natural logs for the ANOVAs. The test for the equality of slopes showed that all slopes differed ($P = <0.0001$ for all combinations). Thus, delaying feeding affected the final fish size and caused a decrement in the growth rate after feeding resumed.

Evaluation of Midgut Cell Height Criterion

For a subset of northern anchovy larvae taken from the treatments where larvae were fed, starved, and feeding was delayed 1 day (S1/F), we compared the number of larvae correctly classified to feeding treatment by the midgut cell height and by the traditional histological index (O'Connell 1976). To define the midgut cell height interval for each feeding treatment, we selected the midpoint between successive cell height means (Table 3) as the interval breakpoint for predicting feeding history from cell height. The midgut cell height was correlated with the histological score (Fig. 3, $n = 38$, $P < 0.001$, t-ratio = 25.85). Both the cell height and the histological score correctly classified all of the subset larvae that were fed to the correct group and 78 and 79% of the starved larvae to the correct group. On the other hand, for the delayed feeding group (S1/F), the midgut cell height was a better predictor of feeding history than the histological score. The midgut measurement classified 78% correctly whereas the histological score classified only 50% correctly.

After the apparent success of this evaluation, we used the midgut cell height data set (Table 1; Fig. 4) to establish the criteria needed to define and calibrate the midgut cell height measurement for predicting feeding history and for calculating starvation rates of anchovy larvae in the sea.

Diet and Midgut Cell Height Categories for Larvae <4.0 mm

We defined the diet and cell height categories for first-feeding larvae (<4.00 mm SL) which are vulnerable to starvation. The height of the

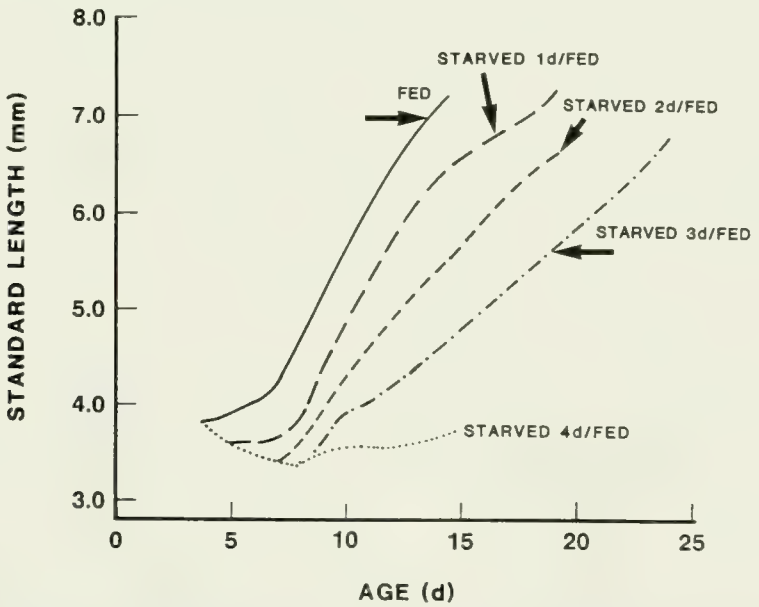

FIGURE 2.—Growth of *Engraulis mordax* larvae under different feeding conditions.

TABLE 3.—Midgut cell height (mght) statistics for six diets by northern anchovy size.

Size Interval (mm)	Fed *n* $\bar{x}$ mght (μm) SD	Starved 1 d/fed *n* $\bar{x}$ mght (μm) SD	Starved 2 d/fed *n* $\bar{x}$ mght (μm) SD	Starved 3 d/fed *n* $\bar{x}$ mght (μm) SD	Starved 1 & 2 d *n* $\bar{x}$ mght (μm) SD	Starved 3 & 4 d *n* $\bar{x}$ mght (μm) SD	All
<4.00	20 20.50 2.27	31 15.56 3.18	33 12.58 2.12	41 11.77 2.44	28 13.48 2.81	24 10.38 2.00	176
4.00–4.99	40 19.47 3.67	18 17.36 3.58	27 15.28 2.51	20 13.68 2.64			105
5.00–5.99	21 20.95 2.71	8 20.63 3.78					29

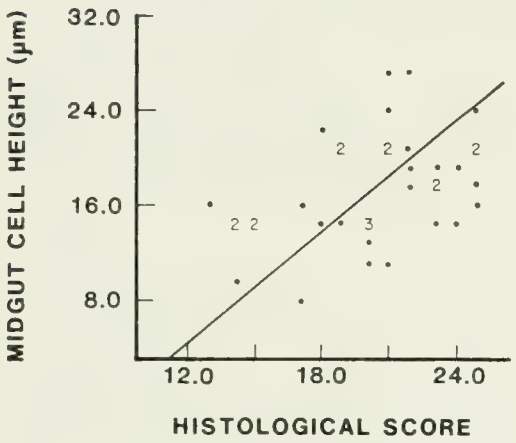

FIGURE 3.—*Engraulis mordax* larvae, regression of midgut cell height measurement on histological score.

midgut cells decreased from the fed to the starved state. The average height of the midgut cells in fed fish <4.00 mm was 20.5 μm. The height averaged 15.6 μm when feeding was delayed one day, 12.6 μm for a 2 d delay and 11.8 μm for a 3 d delay in feeding. The mean midgut height for larvae starved 1 and 2 days was 13.5 μm and for the 3 and 4 d starved group was 10.4 μm (Table 3; Fig. 5).

The height of midgut cells of the fed group (fed) and those where feeding was delayed 1 day (S1/F) was different from all other groups (ANOVA P's < 0.01; Table 4). Fish starved 3 and 4 days (S3&4) also differed from all others (P's < 0.05 level). On the other hand, midgut cell heights of larvae starved 1 and 2 days (S1&2) were not different from those of larvae in which feeding was delayed 2 or 3 days (S2/F and S3/F) (P's = 0.16 and 0.17; Table 4). The t-test matrix indicated four distinct diet and cell height

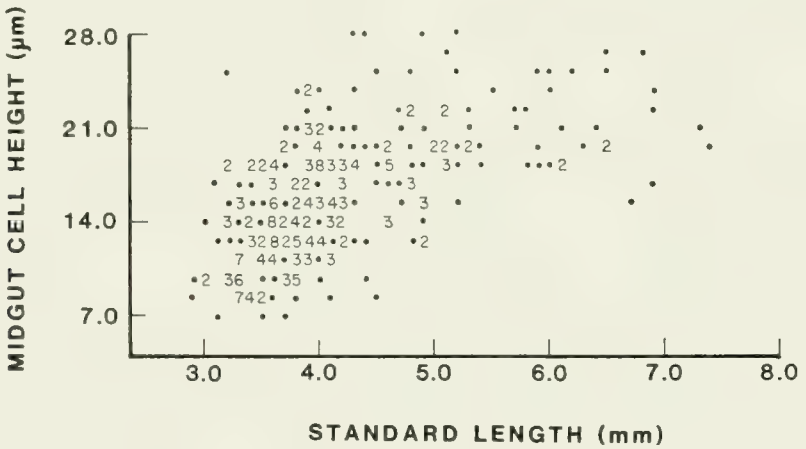

FIGURE 4.—Midgut cell height measurements for *Engraulis mordax* larvae that were raised in the laboratory. Fish were either fed, starved, or feeding was delayed.

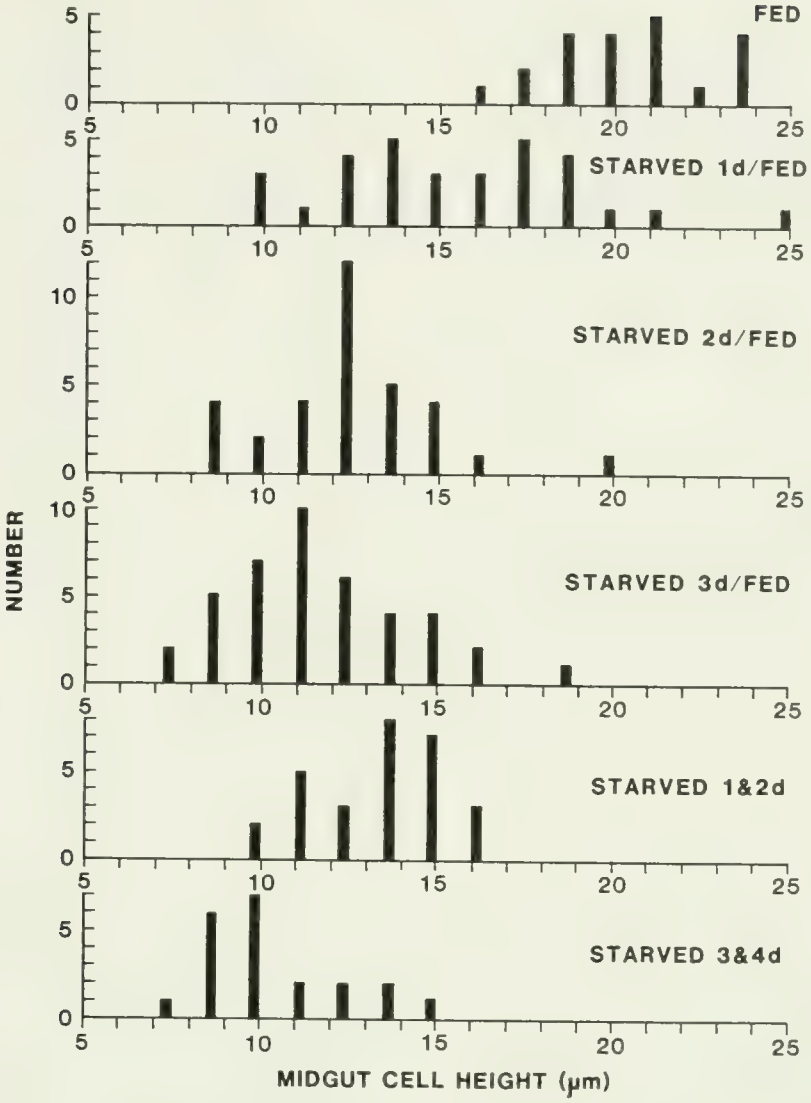

FIGURE 5.—Midgut cell height measurements for *Engraulis mordax* larvae <4.00 mm raised using various feeding conditions.

TABLE 4.—Paired comparison of midgut cell heights for six diets for northern anchovy <4.00 mm SL: *t*-test matrix and probabilities ($P = < 0.01$, **; $P = < 0.05$,*; $P = > 0.05$, value).

		Starved				
	Fed	1 d/fed	2 d/fed	3 d/fed	1 & 2 days	3 & 4 days
Fed	0.0000					
Starved						
1 d/fed	− 6.8438**	0.0000				
2 d fed	−11.1211**	−4.7522**	0.0000			
3 d/fed	−12.7320**	−6.3433**	−1.3731/.17	0.0000		
1 & 2 days	− 9.5331**	−3.1765**	1.4029/.16	2.7802**	0.0000	
3 & 4 days	−13.1632**	−7.4916**	−3.2143**	−2.1187*	−4.3834**	0.0000

categories for first-feeding larvae: 1) a fed category, 2) a category for 1 d delay in feeding (S1/F), 3) an intermediate category (S2/F + S3/F + S1&2), and 4) a starved category (S3&4).

Calibrations for Field Studies

To estimate daily starvation rates in the sea using cell height, an approximation of the dura-

tion or response time for each size, diet, and cell height category is needed. The duration is the number of days that larvae belonging to the size, diet, and cell height category remain within that category. Daily rates in the sea (estimates of numbers of larvae per day) are determined by dividing the number of field-collected larvae classified to each category by the category duration. See the following section on "Applying the Calibration Criteria" for a more detailed explanation of this procedure.

Duration for Fed Category, <4.00 mm SL

Fed larvae began to eat at 3.8 mm (preserved length), yet there was little or no growth for 2 days (Fig. 2). Even though, on the average, the fed anchovy grew at 0.41 mm/d, when the delay in growth was considered, the resulting duration for the <4.00 mm fed group was 2.5 days. Thus it took 2.5 days for the fed fish to move out of this size, diet, and cell height category. This initial lag in growth was reported earlier for northern anchovy (Theilacker 1987).

Durations for Intermediate Categories, <4.00 mm SL

The durations were 5 days for diet groups where feeding was delayed 1 and 2 days (S1/F and S2/F). The group that was starved 3 days before feeding (S3/F) remained within the midgut cell height interval for 8 days (Table 1). The duration for larvae that were starved for 1 and 2 days (S1&2) was 2 days.

Duration for Starved Category, <4.00 mm SL

The duration for the group starved 3 and 4 days (S3&4) was 2 days. Northern anchovy larvae died after starving 3–4 days. No larvae belonging to the starved category were larger than 4.0 mm.

Field Feasibility Study

Because larval fish tissues decompose rapidly due to autolysis (Theilacker 1978; O'Connell 1980), we tested the effects that the prolonged processing periods encountered at sea have on the integrity of the midgut cells. In this study, after 5 minutes in the net, the condition of both formalin- and Bouin's-fixed larval tissues could not be graded using traditional histological criteria due to indistinct nucleoli, diffused nuclei, and intercellular spaces. However, measurement of midgut cell height was still possible after 25 minutes.

The height of the midgut cells, whether measured in formalin- or Bouin's-fixed individuals, showed little change in height over the 25 min processing period (Fig. 6a–d; slope b is not significant from 0; $P = 0.494$ and 0.596 for the formalin group and 0.077 and 0.039 for the Bouin's group, Table 5). Although the height of midgut cells is stable within each diet and 1 mm interval size category (Table 3), we weighted the midgut cell height by fish size for this analysis because it included both fed and starved larvae ranging between 2.8 and 5.6 mm. When the midgut height of fish belonging to all diets was plotted over the 2.8–5.6 mm size range, midgut cell height increased linearly with size (Fig. 4). And, because the fish shrink in the collecting net and the amount of shrinkage is related to the time elapsed in the net, we adjusted fish lengths in this analysis to equal "capture" size using the model developed by Theilacker (1980).

Applying the Calibration Criteria

In practice, when applying this analysis to the field to estimate starvation-induced mortality rates (Owen et al. 1989), it was deemed necessary to use only three diet categories (fed, intermediate, and starved) instead of the four distinct categories determined by ANOVA (Table 4), and discussed earlier. Because the durations were 5 days for both diets where feeding was delayed 1 and 2 days (S1/F and S2/F), there was no need for the S1/F larvae to be a separate, fourth category. Thus we included S1/F in the intermediate category and selected 5 days as an average duration for the <4.00 mm larvae in this category.

The cell-height intervals for the three categories were the midpoints between the means of the group cell heights determined for the laboratory-reared larvae. We regarded all larvae with a midgut height measurement >17.5 μm as belonging to the fed category; the break between the intermediate and starving categories was 11.25 μm. This classification scheme correctly identified 95% of the fed larvae, 77% of the starved larvae, and 74% of the intermediate larvae <4.00 mm SL.

To calculate the starvation rates of northern anchovy larvae in the sea, we measured the length of each field-collected larva (corrected for

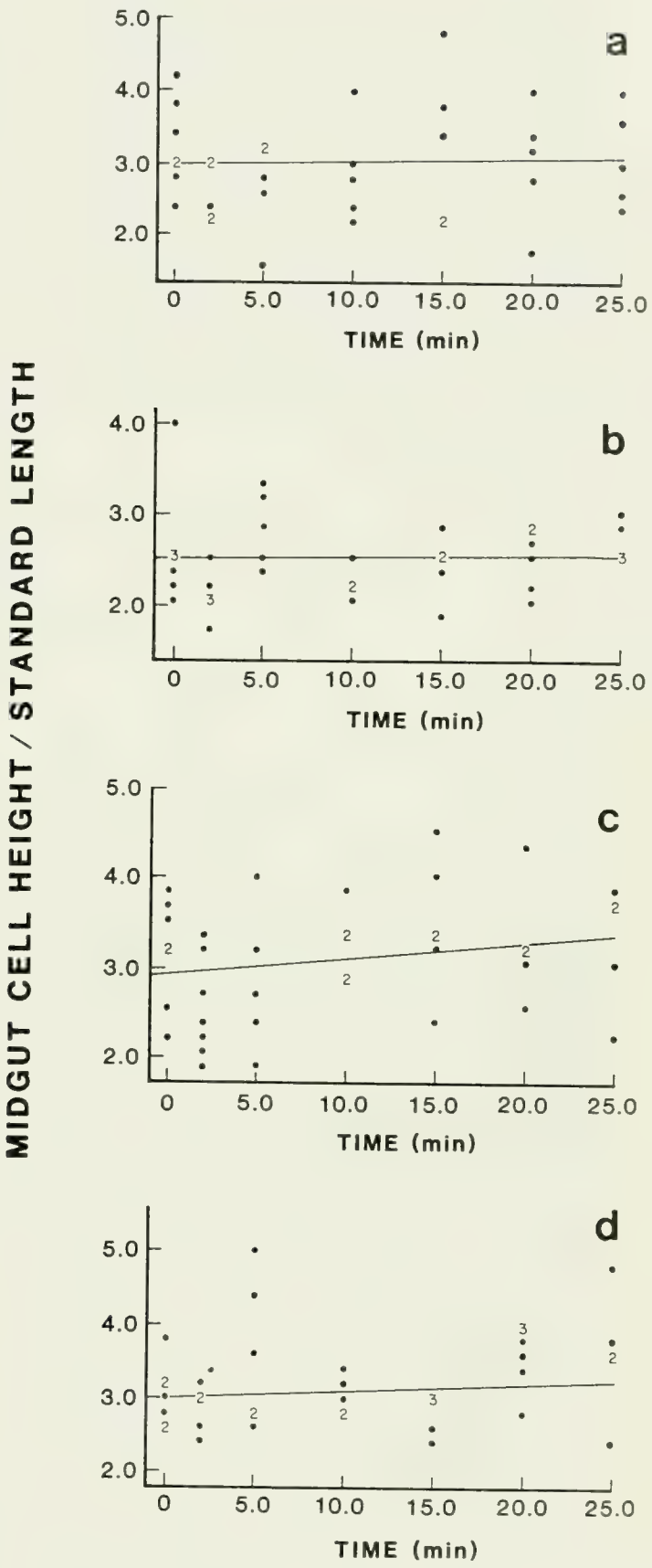

FIGURE 6.—a) Change in midgut cell height measurement over time for formalin-fixed *Engraulis mordax* larvae that were fed. b) Change in midgut cell height measurement over time for formalin-fixed *Engraulis mordax* larvae that were starved. c) Change in midgut cell height measurement over time for Bouin's-fixed *Engraulis mordax* larvae that were fed. d) Change in midgut cell height measurement over time for Bouin's-fixed *Engraulis mordax* larvae that were starved.

shrinkage due to time-in-net and preservation (Theilacker 1980)) and the height of the midgut cells. The adjusted SL and absolute midgut cell height classifies each larva into a size, diet, and midgut cell height category. The numbers of larvae belonging to each category are divided by the category durations to yield the number of larvae per day per category. To estimate the percentage of larvae dying per day due to starvation, the starved category is divided by the total number. An example of these manipulations in Table 5 (taken from Owen 1989; this issue) shows that mortality due to starvation was estimated to be 24%/d for first-feeding anchovy larvae collected off southern California.

(taken on sagittal sections that were prepared for histological examination) defines past feeding history. Kostomarova (1962) also measured the height of intestinal cells of larval fishes to evaluate their state of health. Although she found a relation between fish condition and size of midgut cells, the relation was not quantified. In our study, we establish criteria for discriminating the condition of laboratory-raised larvae using the midgut cell height and for estimating rates of starvation in the field.

To validate this technique, it was necessary to measure the effects on the midgut cells of the prolonged processing periods, commonly encountered at sea. The elapsed time for standard

TABLE 5.—Histological condition of larval northern anchovy off southern California. (From Owen et al. 1989: table 7.)

		INSHORE SITE I				
		Categories				
SL mm		Fed "healthy"	Interme-diate	Starved	Total	%/d
<4.00	Number[1]	28	17	9		
	Duration[2]	2.5	5	2		
	No./d[3]	11.2	3.4	4.5	19.1	24

[1]Number of field-collected larvae belonging to each size, diet, and midgut-cell-height category.
[2]Response times for each size, diet, and midgut-cell-height category (see text)
[3]Number/duration = No./d.

To complete these manipulations for the next size class, 4–<5 mm, fed and intermediate larvae were discriminated using the same cell height measurement, 17.5 μm, and starved larvae did not grow into this size class (Table 3). The duration for the fed category was 2.5 days and for the intermediate category averaged 3 days. The 2.5 d duration for the fed category was obtained by dividing the size-class interval by the growth rate, 0.41 mm/d. Larvae from the delayed-feeding treatments that belonged to the intermediate category outgrew this size class within 2–4 days (Table 1). Some larvae belonging to the group where feeding was delayed 1 day (S1/F) had recovered and entered the fed category by the time they grew to 4.00 mm.

Cell heights cannot be measured for northern anchovy larger than 6 mm SL as the midgut folds, increasing the absorptive area and making cell heights difficult to measure.

DISCUSSION

The height of northern anchovy midgut cells

ichthyoplankton net hauls to 225 m is 21 minutes, and additional time is needed for washing down the net and for sample preservation (Smith and Richardson 1977). To quantify the effect of collecting time and processing time on autolysis, we simulated the net collection and used a matrix of 8 time periods, ranging from 0 to 25 minutes, followed by preservation in either of two fixatives, Bouin's or formalin. Initially, alcohol also was tested because we anticipated using the same fish to study both growth and condition. (80% alcohol is routinely used to preserve otoliths.) Unfortunately, we found alcohol useless for histopathology.

The height of the midgut cells did not change over the 25 m net treatment, but the standard length decreased. Thus, for field collections, it is not necessary to adjust midgut height for time-in-net, but it is important to correct standard length of field-collected larvae for shrinkage in order to allocate the larvae into the correct length categories. The model (Theilacker 1980) used to adjust length was generated for formalin-preserved anchovy. Perhaps the slight

increase noted in the midgut index (midgut cell height/SL) of the Bouin's-fixed specimens (Fig. 6c, d) indicates that the model is overcorrecting for Bouin's. That is, the additional shrinkage caused by fixation (shrinkage in addition to that due to abrasion by the collecting net) is less when Bouin's is used for the final fixative than when formalin is used. This logic, however, is hard to reconcile because Bouin's, made with 20% formalin, is stronger than the 5% formalin solution we used.

Starved fish may be shrinking more during the net treatment than their fed counterparts, further complicating the interpretation of the shrinkage adjustment. But we cannot be certain that this occurred because we did not follow individual larvae during the net treatment. Yet there was a significant decrease in length of starved larvae when the adjusted lengths (corrected to "live length") were regressed and plotted over time (Fig. 7b; Table 6). The decrease in length was not evident for the fed larvae (Fig. 7a). This apparent difference in shrinkage rates between fed and starved larvae needs to be tested.

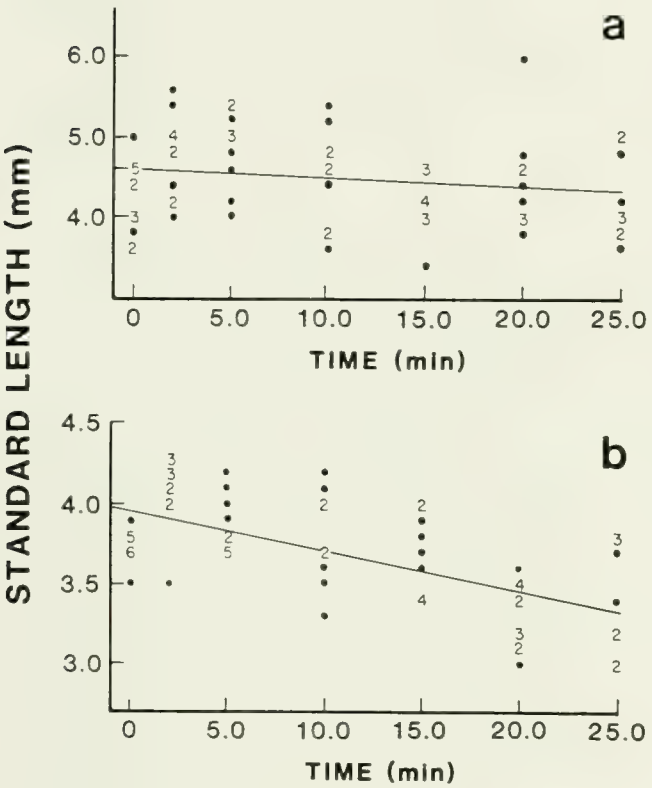

FIGURE 7.—a) Change in standard length over time for fed *Engraulis mordax* larvae that were fixed in formalin and Bouin's. b) Change in standard length over time for starved *Engraulis mordax* larvae that were fixed in formalin and Bouin's.

TABLE 6.—Coefficients for regressions of midgut indexes (midgut cell height/adjusted standard length (mght/SL)) and of adjusted standard length (SL) with elapsed time-in-net (t).

Diet	Measurement	Fixative	Mght/SL = a + bt a	b	P	Reference figure
Fed	Mght/SL	5% formalin	2.8941	0.0092	0.494	6a
Starved	Mght/SL	5% formalin	2.4869	0.0041	0.596	6b
Fed	Mght/SL	Bouin's	2.8961	0.0212	0.077	6c
Starved	Mght/SL	Bouin's	2.9839	0.0231	0.039	6d
Fed	SL	Formalin & Bouin's	3.9605	−0.0251	0.000	7a
Starved	SL	Formalin & Bouin's	4.5813	−0.0124	0.079	7b

Incidental information from delayed feeding experiments (Table 1) revealed that, depending on diet, age of 5 mm northern anchovy ranged between 9 and 19 days. This 10 d range in age at size (due to feeding history) has important implications for size-at-age mortality estimates.

In conclusion, our study indicates that the absolute midgut cell height of northern anchovy larvae is a practical criterion to use for estimating rates of starvation. The cell height measurement yields reliable estimates of feeding history, is resistant to autolysis, and is reliable in formalin-fixed specimens. Thus, the special ichthyoplankton tows and preservatives required for a histopathological index are not needed when the midgut index is used. The midgut index is as sensitive to nutritional conditions as the histological index and does not require the rigorous calibration needed for the morphometric technique (Theilacker 1986; Setzler-Hamilton et al. 1987). Also the midgut character is much easier and faster to measure than scoring the histological features of northern anchovy tissues, and it does not require a solid background in histology for the person scoring. Because of these features, the midgut index is practical for routine estimates of starvation rates of larvae in the sea. In addition, unlike previous methods, the duration of tow is not a constraint because the character does not degrade with time and a sample representative of the water column can be taken.

ACKNOWLEDGMENTS

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Comparative Growth, Mortality, and Energetics of Marine Fish Larvae: Temperature and Implied Latitudinal Effects

Edward D. Houde

ABSTRACT: Vital rates and energetics of marine fish larvae were examined in relation to temperature to determine if recruitment potential and spawning strategies might vary as a consequence of differences in these traits among species. Literature-derived values of growth rates, mortality rates, larval stage durations, gross growth efficiencies, and oxygen uptakes were considered. Results were presumed to reflect latitudinal variation among species. Instantaneous daily growth and mortality rates each increased approximately 0.01 per °C increase in temperature. But, there was no significant regression of gross growth efficiency on temperature (mean K_1 = 0.29), indicating no latitudinal relationship. The large increases in growth rate at high temperatures must be supported by increased food consumption, not increased growth efficiency. Oxygen uptakes also increased significantly in relation to temperature, but relatively slowly compared to growth rates. Larval stage duration was inversely related to growth rate. The potential variability in growth rate was observed to increase with temperature, but the opposite trend was observed for stage duration. Thus, stage durations tended to be both long and potentially variable in high latitudes. Because of these characteristics it is suggested that early life, density-dependent regulation is more probable in high than in low latitudes. The required ingestion to support average growth rate increased threefold in the 10°–30°C range, indicating that fish larvae in warm seas may be more likely to starve than larvae in cold seas. Spawning in low latitudes often is protracted with frequent batches in contrast to spawning in high latitudes, where seasons are brief, with one or a few batches. The different strategies may have been selected and maintained to counter energetic and dynamic constraints in the larval stage.

Variability in growth and mortality rates of marine fish larvae can cause fluctuations in recruitment levels. The two processes, growth and death, may interact and can be viewed as a "single process" in early life (Cushing 1975). In reviewing larval mortality rates, it is apparent that not only are rates high but they range widely (Dahlberg 1979; McGurk 1986). Growth rates also are variable, both among and within species, which could cause significant fluctuations in recruitment levels through effects on larval stage duration (Houde 1987). If variation in the magnitude of larval growth or mortality were predictable, for example, in relation to latitude, the consequences of it might be discernible in life history strategies or in physiological adaptations of fishes from different temperature zones.

Objectives of this paper are to compare vital rates and energetics parameters of marine fish larvae, and to discuss results in the context of spawning strategies and possible mechanisms in the larval stage that may regulate the recruitment process. A cursory examination of literature indicated that teleost larval growth and mortality rates increased relative to temperature and that temperature could, in a general way, be equated to latitude. A review and comparative analysis were undertaken to define the relationships between temperature and the larvae 1) growth rates, 2) stage duration, 3) mortality rates, 4) growth efficiency, and 5) oxygen uptakes. From the analysis, it was possible to estimate cohort net survivorships, to develop energy budgets, and to estimate ingestion requirements of first-feeding larvae over the range of temperatures that was surveyed. The likelihood of starvation by marine fish larvae from low and high latitudes was considered. Because spawning strategies of marine fishes may be linked to larval dynamics and energetics, results also were considered in relation to dominant spawning patterns in warm and cold seas.

METHODS

Literature was reviewed to obtain data for the analyses. Relationships and variables that were

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analyzed are defined in Table 1. Analyses were confined to feeding-stage larvae of marine fishes and to a few anadromous species. Salmonid fishes, which lack a typical larval stage, were not included.

TABLE 1.—Relationships that were analyzed and abbreviations that are used in text.

T	Temperature, °C
G	Weight-specific growth rate, d^{-1}
D	Stage duration, defined as days from hatching to metamorphosis, d
Z	Instantaneious daily mortality coefficient, d^{-1}
K_1	Gross growth efficiency, G/I
I	Weight-specific ingestion rate, d^{-1}
Q_{O_2}	Weight-specific oxygen uptake, μL O_2/mg/h
N_{met}	Net survivorship; fraction of a cohort expected to survive from hatching to metamorphosis

Growth

Weight-specific growth rates (G) of larvae were obtained from laboratory and field studies. Growth coefficients were taken directly from published work, when available, or calculated from the data. In a few cases, length-weight relationships were used to convert growth-in-length data to growth-in-weight. Weight-specific growth data for larvae of some commonly studied species were unavailable and those species could not be included in analyses. Weight-specific growth rates are

$$G = \frac{(\ln W_t - \ln W_0)}{t}$$

where W_0 and W_t are dry weights of larvae at hatch and at the end of a growth period of t days' duration.

A linear regression was fitted to express the relationship of weight-specific growth rates on temperature. Because both G and T for a species sometimes had a considerable range reported in the literature, the midpoints of reported G and T values were selected arbitrarily as the data for each species in the regression analysis. A Q_{10} was estimated from predicted values of G in the range 5°–30°C.

Stage Duration

Stage duration (D) was defined as days from hatching to metamorphosis. As such, it is inversely proportional to weight-specific growth rate (G) and dependent upon species-specific weight at metamorphosis. Stage duration was calculated from the literature-derived data on G, dry weights at hatch (W_0), and dry weights at metamorphosis (W_m)

$$D = \frac{(\ln W_m - \ln W_0)}{G}.$$

A power regression was fitted, in which the geometric midpoint, i.e., antilog [($\log_{10}$ low D + $\log_{10}$ high D) * ½] of the estimated range of D for each species was regressed on the estimated midpoint of temperature, to describe the relationship between stage duration and temperature.

Mortality

Instantaneous daily mortality coefficients (Z) of post-yolk-sac larvae were obtained from published field studies in which the rates had been determined or could be calculated from the authors' estimated abundances-at-age. Much of the mortality data was obtained from summaries and references in papers by Dahlberg (1979) and McGurk (1986), supplemented with Z estimates from additional and more recent sources.

A linear regression of the midpoints of the estimated range of Z on the midpoints of T for each species was fitted to describe the relationship between $Z$and T.

Relationship Between Mortality and Growth Rates

Solution of the equation for growth rate on temperature in terms of temperature and its substitution into the equation for mortality rates on temperature yielded an expression relating mortality rates to growth rates.

Net Survivorship

Based on the estimates of growth rates, stage duration, and mortality rates predicted from the regressions, the proportion of a cohort expected to survive to metamorphosis (N_{met}) was calculated for 10°, 20°, and 30°C. The percentage cohort survivorship at each of the temperatures was calculated from the exponential relationship

$$100\, N_{met} = e^{-ZD}.$$

Effects on survivorship of decreases in G and

increases in Z also were determined at those three temperatures.

Growth Efficiency

Gross growth efficiency (K_1) is the proportion of ingestion that goes to growth;

$$K_1 = G/I\ ,$$

where G is the weight-specific growth rate and I is the weight-specific ingestion rate. Growth efficiencies and temperatures (T) in published reports were examined. An attempt was made to fit a linear regression to midpoints of K_1 regressed on midpoints of T for species where data were available.

Because $I = G/K_1$ and the regression relationship between G and T had been defined, weight-specific ingestion rate also could be related to temperature. That expression was applied to estimate the weight-specific ingestion rate required to attain mean, among-species growth rates in relation to temperature. It was assumed that an average food particle for a first-feeding larva weighed 0.25 μg dry weight. Then, the number of particles required to attain average growth rate and the consequences of changes in temperature on that requirement were explored. The regression relationship between I and G also was examined to determine the rate of increase in ingestion necessary to support increased growth.

Metabolism

The Q_{O_2}, i.e., weight-specific oxygen uptakes, were obtained for marine fish larvae where data were available. Values were taken directly from literature or derived if the relationship between oxygen uptake and larval dry weight was reported. Values used here were confined to those for feeding or end-of-yolk-sac stage larvae. The midpoints in the range of Q_{O_2} for a species were regressed on the midpoints of the temperature values to obtain a relationship between weight-specific oxygen uptake and temperature. A Q_{10} was derived from the predicted values of Q_{O_2} in the 5°–30°C range.

Energy Budgets

Energy budgets for average first-feeding larvae at 10°, 20°, and 30°C were developed from the information and relationships on growth rates (G), oxygen uptake (Q_{O_2}), and ingestions (I). Budgets were expressed as

$$I = G + M + F$$

where M is metabolism and F is feces. The Q_{O_2} was converted to M using an oxycalorific equivalent of 0.00463 cal/μL O_2 (Brett and Groves 1979). The oxygen uptake estimates reported in the literature generally were made on "resting" or anesthetized larvae. These estimates were presumed to represent routine metabolism. For the energy budgets, the reported Q_{O_2} values were multiplied by 2.0 to estimate active metabolism for 12 hours of the day, the time that a larva was assumed to swim actively while feeding (i.e., daylight hours). The estimated Q_{O_2} from the regression relationship was assumed to apply during the remaining 12 hours. The 2.0 multiplier is commonly used, but may be conservative (Brett and Groves 1979). If metabolism has been underestimated, the absolute values of budget components are in error but relative effects of temperature on the larval energy budgets still will be expressed.

Both ingestion rates and growth rates were converted from dry weight to calories by assuming an equivalency of 5,000 cal/g dry weight. Values for feces in the energy budgets were obtained by difference. Energy budgets were expressed both in absolute and relative (i.e., percent) terms. After the energy budgets had been determined, assimilation efficiencies, $A = (G + M)/I$, and net growth efficiencies, $K_2 = G/(G + M)$, were derived and compared among temperatures (see Table 8).

RESULTS

Growth

Weight-specific growth coefficients ranged from <0.01 to >0.55, indicating a widely varying potential for growth among species of marine fish larvae that was strongly related to temperature and, presumably, latitude (Table 2; Fig. 1). Relative growth-in-weight ranged from <1% to >73% d^{-1}. The regression of midpoint G on midpoint T for 27 species indicated an approximate 0.01 increase in G for each degree increase in T.

$$G = -0.0036 + 0.0094\,T$$

$$r^2 = 0.57 \qquad S_b = 0.0016. \qquad (1)$$

TABLE 2.—Weight-specific growth coefficients (G) from laboratory and field-estimated growth rates of marine fish larvae. Temperatures (T), dry weight ranges, and mid-points of estimated G and T also are given. Values were taken directly from published results, calculated from the authors' data or calculated from available length-weight relationships.

Species	Temperature		Dry weight range (mg)	Growth coefficient (G)		References
	Range	Midpoint		Range	Midpoint	
Clupea harengus CH	06.0–17.0	11.5	0.06–100.00	<0.01–0.12	0.065	McGurk (1984) and numerous references therein; Gamble et al. (1985); Kiorboe and Munk (1986); Kiorboe et al. (1987)
Chanos chanos CC	25.0–29.0	27.0	0.25–60.00 (wet wts)	0.12–0.17	0.145	Liao et al. (1979); Duray and Bagarinao (1984)
Anchoa lamprotaenia ALa	26.0	26.0	0.02–0.06	0.21	0.210	Chitty (1981)
Anchoa mitchilli AM	23.0–31.0	27.0	0.01–6.00	0.15–0.35	0.250	Houde (1977d, 1978); Houde and Schekter (1981); Leak and Houde (1987); Houde (unpub. data)
Engraulis mordax EM	13.0–16.0	14.5	0.02–0.50	0.14–0.30	0.220	Hunter (1976); Methot and Kramer (1979); Smith (1985); Theilacker (1987)
Gadus morhua GM	4.0–11.0	7.5	0.05–3.00	0.02–0.12	0.070	Laurence (1978); Buckley (1979); Laurence et al. (1981); Gamble and Houde (1984); Øiestad (1985); Buckley and Lough (1987)
Melanogrammus aeglefinus MA	4.0–9.0	6.5	0.07–2.90	0.01–0.13	0.070	Laurence (1974, 1978); Laurence et al. (1981); Bergen et al. (1985); Buckley and Lough (1987); Buckley et al. (1987)
Merluccius productus MP	10.5–15.0	13.0	~0.04–~1.80	—	0.060	Bailey (1982)
Theragra chalcogramma TC	5.0–9.5	7.0	0.04–33.50	0.02–0.13	0.075	Hamai et al. (1974); Clarke (1984); Nishimura and Yamada (1984); Walline (1985); Bailey and Stehr (1986); Kendall et al. (1987)
Menidia menidia MM	19.0–21.0	20.0	~0.50–8.90 (wet wts)	~0.13	~0.130	Beck and Poston (1980)
Menidia peninsulae MP	20.0–30.0	25.0	0.03–2.24	0.08–0.25	0.165	McMullen and Middaugh (1985)
Morone americana MAm	13.0–21.0	17.0	0.02–0.09	0.03–0.18	0.105	Margulies (1986)
Morone saxatilis MS	12.0–22.5	17.0	0.15–15.00	0.09–0.19	0.140	Dey (1981); Eldridge et al. (1981); Rogers and Westin (1981); Eldridge et al. (1982); Houde and Lubbers (1986); Chesney (1986)
Dicentrarchus labrax DL	13.0–20.0	16.5	0.09–~2.80	0.07–0.18	0.125	Girin (1975); Girin et al. (1975); Barahona-Fernandes and Girin (1977); Barahona-Fernandes (1978,1979); Gatesoupe and Luquet (1981); Gatesoupe and Robin (1982)

TABLE 2.—*Continued.*

Species	Temperature		Dry weight	Growth coefficient (*G*)		References
	Range	Midpoint	range (mg)	Range	Midpoint	
Haemulon flavolineatum HF	~25.0–~30.0	~27.5	0.02–10.00	~0.24–~0.41	~0.325	McFarland et al. (1985); Saksena and Richards (1975)–data on *H.plumieri*, used to approximate *H. flavolineatum*.
Archosargus rhomboidalis AR	23.0–29.0	26.0	0.01–4.20	0.21–0.41	0.310	Houde (1975, 1978); Stepien (1976); Houde and Schekter (1981)
Pagrus major PM	17.0–23.5	20.0	0.05–13.70 (wet wts)	0.06–0.33	0.195	Fushimi and Nakatani (1977); Kitajima et al. (1980); Fukusho et al. (1984); Kuronuma and Fukusho (1984)
Sparus aurata SA	15.0–20.0	17.5	~0.02–~10.00	0.10–0.14	0.120	Divanach (1985); Tandler and Helps (1985)
Cynoscion nebulosus CN	24.0–32.0	28.0	0.02–1.60	0.16–0.57	0.365	Taniguchi (1979, 1981)
Ammodytes americanus AA	0.0–10.0	5.0	0.04–10.00	<0.01–0.12	0.060	Buckley et al. (1984); Smigielski et al. (1984); Monteleone and Peterson (1986); Buckley et al. (1987)
Scomber japonicus SJ	17.0–22.0	19.5	0.03–34.45	0.25–0.43	0.340	Hunter and Kimbrell (1980)
Scomber scombrus SSc	15.0	15.0	0.05–2.23	0.10–0.18	0.140	Buckley et al. (1987)
Paralichthys dentatus PD	18.0	18.0	–	0.07	0.070	Buckley and Dillman (1982)
Scophthalmus maximus SM	13.0–18.0	15.5	0.04–10.00	0.10–0.25	0.175	Jones et al. (1974); Kuhlmann et al. (1981); Person LeRuyet et al. (1981); Paulsen et al. (1985); Quantz (1985)
Pseudopleuronectes americanus PA	2.0–10.0	6.0	0.01–1.45	0.02–0.14	0.080	Laurence (1975,1977); Buckley (1982); Cetta and Capuzzo (1982)
Achirus lineatus AL	28.0	28.0	0.01–0.20	0.16–0.33	0.245	Houde (1977d, 1978); Houde and Schekter (1981)
Solea solea SS	17.0–19.0	18.0	0.30–8.00 (wet wts)	0.10–0.21	0.155	Girin (1979); Fuchs (1982); Gatesoupe and Luquet (1982)

Estimated G increased from 0.04 at 5°C to 0.28 at 30°C. The Q_{10}, calculated from the predicted G, was 2.11 over the range 5°–30°C.

Some species deviated considerably from the average regression relationship (Fig. 1; Table 2). For example, Pacific mackerel, *Scomber japonicus*, larvae had a high growth rate; however, Atlantic mackerel, *S. scombrus*, did not deviate much from the regression line. Northern anchovy, *Engraulis mordax*, also had relatively high growth rate, while herring, *Clupea harengus*, Pacific hake, *Merluccius productus*, and milkfish, *Chanos chanos*, had lower than expected growth rates for their respective temperature. The observed variation in growth rates was greatest at high temperature (Fig. 1), indicating that fish larvae at high temperatures and, more generally, in low latitudes have potentially more variable growth rates than do larvae at low temperatures from high latitudes.

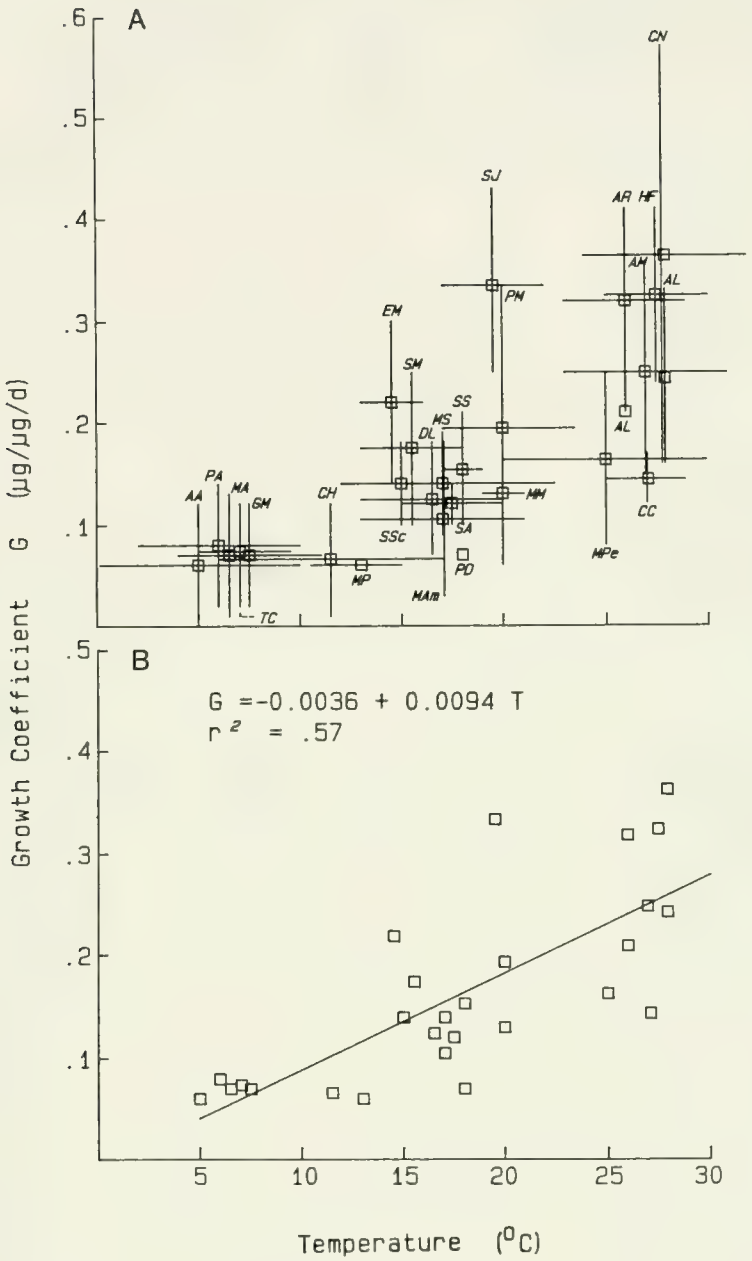

FIGURE 1.—Weight-specific growth coefficients (G) of marine fish larvae in relation to temperature (T). A. Ranges and midpoints of reported G and T values. Data, letters designating species and references are from Table 2. B. Regression relationship of midpoint G on midpoint T.

Stage Duration

Larval stage duration ranged from 10 days to >550 days, based on the reported growth rates (Table 3; Fig. 2). The regression relationship for 27 species indicated that stage duration (D) declines rapidly as temperature (T) increases.

$$D = 952.5T^{-1.0752}$$

$$r^2 = 0.70 \qquad S_b = 0.1418. \qquad (2)$$

Predicted stage duration ranged from 25 days at 30°C to >165 d at 5°C. The variability in stage duration was greatest at low tempera-

TABLE 3.—Estimated larval stage durations (D) from laboratory- and field-estimated growth rates, and weights at metamorphosis for marine fish larvae. Temperatures (T), and midpoints of D and T also are given. Values were derived from published results cited for each species in Table 1.

Species	Temperature		Hatch and metamorphosis dry weight (mg)		Stage duration (d)	
	Range	Midpoint	W_0	W_m	Range	Geometric midpoint
Clupea harengus CH	6.0–17.0	11.5	0.090	25.0	46.9–>550	160.6
Chanos chanos CC	25.0–29.0	27.0	0.05	25.0	36.6–51.8	43.5
Anchoa lamprotaenia ALa	26.0	26.0	0.02	25.0	34.0	34.0
Anchoa mitchilli AM	23.0–31.0	27.0	0.015	25.0	21.2–49.5	32.4
Engraulis mordax EM	13.0–16.0	14.5	0.020	25.0	23.8–50.9	34.8
Gadus morhua GM	4.0–11.0	7.5	0.050	7.0	41.2–247.1	100.9
Melanogrammus aeglefinus MA	4.0–9.0	6.5	0.070	7.0	35.4–460.5	127.7
Merluccius productus MP	10.5–15.0	13.0	0.04	7.0	88.0	88.0
Theragra chalcogramma TC	5.0–9.5	7.0	0.04	10.0	42.5–276.1	108.3
Menidia menidia MM	19.0–21.0	20.0	0.10	10.0	35.4	35.4
Menidia peninsulae MP	20.0–30.0	25.0	0.03	10.0	23.2–72.6	41.0
Morone americana MAm	13.0–21.0	17.0	0.02	10.0	34.5–207.2	84.5
Morone saxatilis MS	10.0–22.5	17.0	0.20	15.0	22.7–48.0	33.0
Dicentrarchus labrax DL	13.0–20.0	16.5	0.06	10.0	28.4–73.1	45.6
Haemulon flavolineatum HF	~25.0–~30.0	~27.5	~0.02	~7.0	14.3–24.4	18.7
Archosargus rhomboidalis AR	23.0–29.0	26.0	0.015	7.0	15.0–29.3	21.0
Pagrus major PM	17.0–23.5	20.0	0.01	7.0	19.9–109.2	46.6
Sparus aurata SA	15.0–20.0	17.5	0.02	7.0	41.8–58.6	49.5
Cynoscion nebulosus CN	24.0–32.0	28.0	0.02	7.0	10.3–36.6	19.4
Ammodytes americanus AA	0.0–10.0	5.0	0.04	10.0	46.0–>550	159.1
Scomber japonicus SJ	17.0–22.0	19.5	0.035	10.0	13.2–22.6	17.3
Scomber scombrus SSC	15.0	15.0	0.05	10.0	29.4–53.0	39.5
Paralichthys dentatus PD	18.0	18.0	~0.05	~7.0	98.8	98.8
Scophthalmus maximus SM	13.0–18.0	15.5	0.04	20.0	24.9–62.1	39.3
Pseudopleuronectes americanus PA	2.0–10.0	6.0	0.01	1.0	32.9–230.3	87.0

TABLE 3.—*Continued.*

Species	Temperature		Hatch and metamorphosis dry weight (mg)		Stage duration (*d*)	
	Range	Midpoint	W_0	W_m	Range	Geometric midpoint
Achirus lineatus AL	28.0	28.0	0.101	2.0	16.0–33.1	23.0
Solea solea SS	17.0–19.0	18.0	0.05	8.0	24.2–50.8	35.1

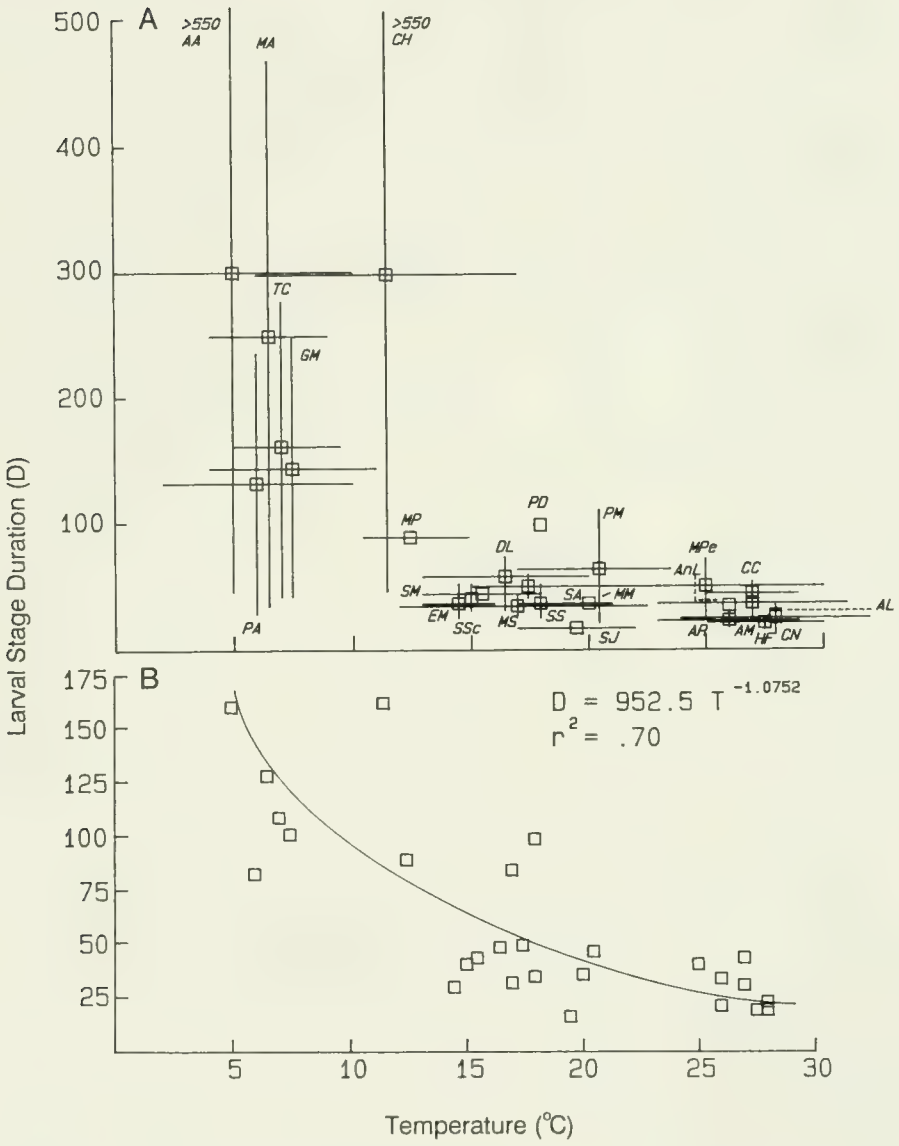

FIGURE 2.—Stage durations (D) of marine fish larvae in relation to temperature (T). A. Ranges and midpoints of D and T values. Data and letters designating species are from Table 3. References are in Table 1. B. Regression relationship of geometric midpoint D on midpoint T.

tures (Fig. 2), indicating more scope for stage duration at low temperatures and presumably in high latitudes. This result was opposite to that observed for growth rate, in which there was more variability at high temperatures (Fig. 1).

Mortality

Mortality coefficients of feeding-stage larvae reported for 22 species ranged from $Z = 0.01$ to 0.69 d^{-1}, equivalent to 1–50% d^{-1} mortality rates (Table 4; Fig. 3). Predicted mortality rate (Z) increased approximately 0.01 per degree increase in temperature (T).

$$Z = 0.0256 + 0.0123\,T$$

$$r^2 = 0.41 \qquad S_b = 0.0034. \tag{3}$$

Estimated Z increased from 0.09 at 5°C to 0.40 at 30°C.

Although quite variable among species, the relationship between mortality rate and temperature is significant ($P < 0.01$). Only Atlantic mackerel appeared to be an outlier from the regression line (Fig. 3); its observed mortality rate was higher than expected for species in the 15–20°C range.

Relationship Between Mortality and Growth Rates

The derived relationship between mortality rate (Z) and growth rate (G) for marine fish larvae was

$$Z = 0.0303 + 1.3085\,G. \tag{4}$$

Also, from predicted G and Z in Equations (1) and (3), it is apparent that the ratio G/Z increases at high T.

T (°C)	$\dot{G}$	$\dot{Z}$	G/Z
5	0.043	0.087	0.494
15	0.137	0.210	0.652
30	0.278	0.395	0.704

Despite the elevated mortality rates suffered by marine fish larvae at high temperatures, their growth potential may allow such larval populations to accumulate biomass and to survive at relatively high rates when feeding conditions are favorable.

Net Survivorship

Predicted net survival at metamorphosis increased by an approximate factor of nine as temperature increased from 10° to 30°C.

	10°C	*20°C*	*30°C*
G (d^{-1})	0.0904	0.1844	0.2784
D (d)	80.11	38.02	24.58
Z (d^{-1})	0.1486	0.2716	0.3946
$100\,N_{met}$ (%)	0.0007	0.0033	0.0061

The effects on N_{met} of a 10% decline in G, a 10% increase in Z, or a combination of 10% decline in G and 10% increase in Z were large.

G *declines 10%*

	10°C	*20°C*	*30°C*
G (d^{-1})	0.0814	0.1660	0.2506
D (d)	88.97	42.23	27.31
Z (d^{-1})	0.1486	0.2716	0.3946
$100\,N_{met}$ (%)	0.0002	0.0010	0.0021

Z *Increases 10%*

	10°C	*20°C*	*30°C*
G (d^{-1})	0.0904	0.1844	0.2784
D (d)	80.11	38.02	24.58
Z (d^{-1})	0.1635	0.2988	0.4341
$100\,N_{met}$ (%)	0.0002	0.0012	0.0023

G *declines 10% and* Z *increases 10%*

	10°C	*20°C*	*30°C*
G (d^{-1})	0.0814	0.1660	0.2506
D (d)	88.97	42.23	27.31
Z (d^{-1})	0.1635	0.2988	0.4341
$100\,N_{met}$ (%)	0.00005	0.0003	0.0007

Effects on percent larval survival at metamorphosis ($100\,N_{met}$) of declining growth rates or increasing mortality rates are greater at low than at high temperatures, a consequence of the long stage durations at low temperature and their dependency on growth rate. Calculated ratios of N_{met} from the examples given above, termed relative survival, compared to those *expected* from the regression relationships at average G, D and Z, are

	Relative Survival		
Example	*10°C*	*20°C*	*30°C*
Expected G, D, Z	1.00	1.00	1.00
G declines 10%	0.27	0.32	0.34
Z increases 10%	0.30	0.36	0.38
G declines 10% and Z increases 10%	0.07	0.10	0.12

TABLE 4.—Instantaneous daily mortality coefficients (Z) from field estimates of reported mortality rates of marine fish larvae in relation to temperatures (T). Estimates here are for feeding-stage larvae only.

	Temperature (°C)		Mortality coefficient (Z)		
Species	Range	Midpoint	Range	Midpoint	References
Alosa sapidissima AS	19.0–23.0	21.0	0.11–0.30 (10–18 mm larvae)	0.210	Crecco et al. 1983
Clupea harengus CH	6.0–17.0	11.5	0.01–0.46	0.235	Graham and Townsend 1985; McGurk 1986; Lough et al. 1985
Etrumeus teres ET	18.0–26.5	22.5	0.13	0.130	Houde 1977a
Harengula jaguana HJ	21.0–31.0	26.0	0.28	0.280	Houde 1977c
Opisthonema oglinum OO	22.5–30.5	26.5	0.21–0.26	0.235	Houde 1977b
Sardinella aurita SA	21.0–27.0	24.0	0.45	0.450	Conand 1977
Sardinops melanosticta SM	11.1–19.1	15.1	0.13	0.130	Nakai and Hattori 1962
Sardinops sagax SS	15.5–18.0	16.4	0.10	0.100	Lenarz 1973
Anchoa mitchilli AM	24.0–31.0	27.5	0.30–0.45	0.375	Leak and Houde 1987
Engraulis japonica EJ	16.0–18.0 (from other literature)	17.0	0.30	0.300	Hiyashi 1966
Engraulis mordax EM	12.0–20.0	16.0	0.16–0.22	0.190	Hewitt and Methot 1982; Smith 1985; McGurk 1986
Melanogrammus aeglefinus MA	4.0–9.0	6.5	0.11	0.110	Jones 1973
Micromesistius poutassou MP	2.0–15.0 (from other literature)	8.5	0.15	0.150	Bailey 1974
Morone saxatilis MS	12.0–22.5	17.0	0.13–0.21	0.170	Dey 1981
Trachurus symmetricus TS	15.0–16.5	16.0	0.18 (rate estimated at 30 d posthatch)	0.180	Hewitt et al. 1985
Archosargus rhomboidalis AR	22.0–29.0	25.5	0.43	0.430	Chavance et al. 1984
Cynoscion nebulosus CN	24.0–31.0	27.5	0.36–0.64	0.500	Peebles and Tolley 1988
Scomber japonicus SJ	13.0–23.0	18.0	0.14	0.140	Watanabe 1970
Scomber scombrus SSc	14.0–20.0	17.0	0.35–0.69	0.520	Sette 1943; Kendall and Gordon 1981; Ware and Lambert 1985
Sebastes spp. Ssp	3.5–12.5	8.0	0.05–0.07	0.060	Anderson 1984
Pleuronectes platessa PP	1.0–8.0	4.5	0.02–0.08	0.050	Harding and Talbot 1973; Bannister et al. 1974; Harding et al. 1978
Pseudopleuronectes americanus PA	3.0–14.0	8.5	0.23	0.230	Pearcy 1962a, 1962b

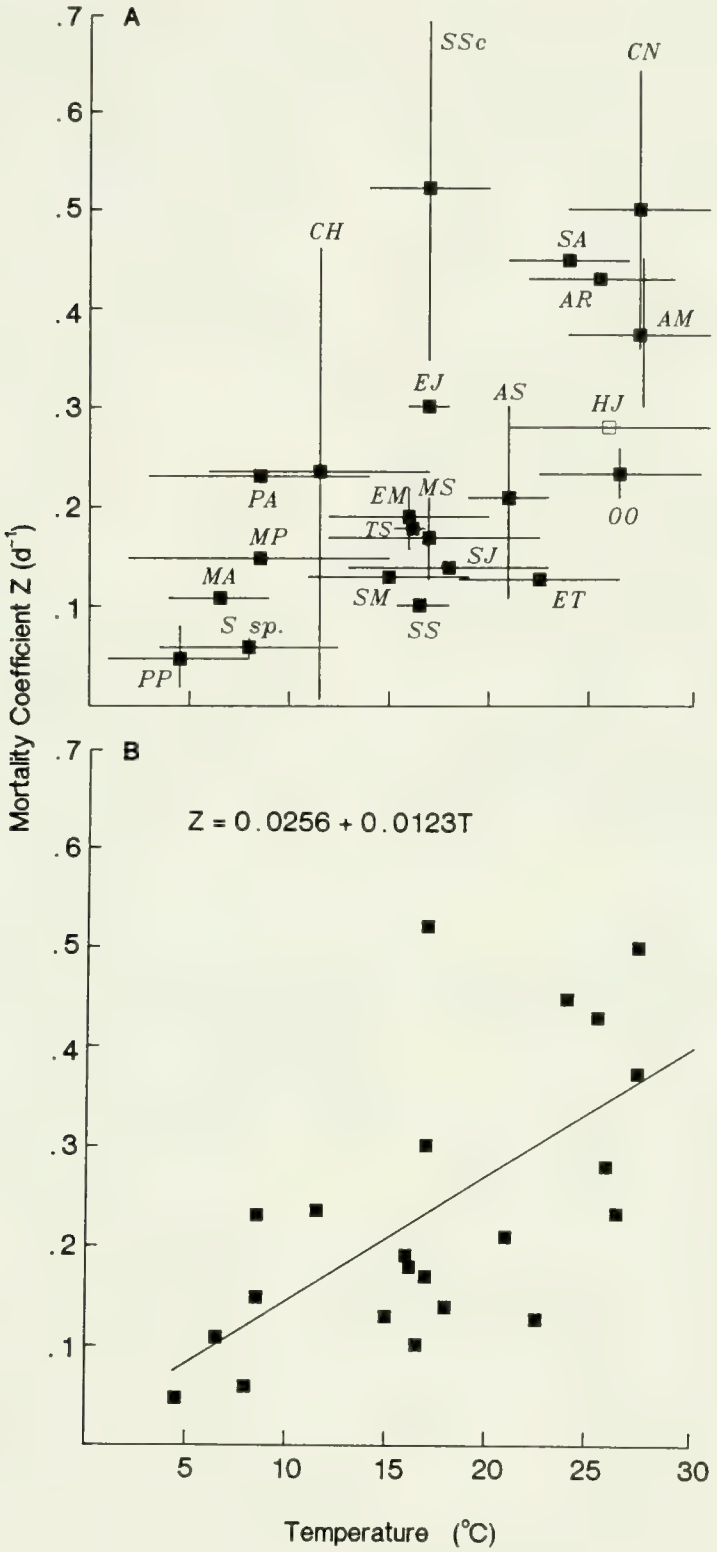

FIGURE 3.—Instantaneous mortality coefficient (Z) of marine fish larvae in relation to temperature (T). A. Ranger and midpoints of Z and T values. Data, letters designating species and references are from Table 4. B. Regression relationship of midpoint Z on midpoint T.

It is important to note that a 10% change in either Z or G will have potentially large effects on survivorship at any temperature.

Growth Efficiency and Ingestion

There was no significant relationship between growth efficiency and temperature (Table 5; Fig. 4) for 10 species where data were adequate for analysis. Mean K_1, with 0.95 confidence limits, is 0.29 ± 0.06, a value equal to that of juvenile, carnivorous fishes (Brett and Groves 1979). One species, European seabass, *Dicentrarchus labrax*, had reported K_1 well above the mean. Two species, winter flounder, *Pseudopleuronectes americanus*, and summer flounder, *Paralichthys dentatus*, had K_1 below the mean. For some species, a large range of potential K_1 was reported (Fig. 4), indicating that estimates of growth efficiency may vary widely in relation to environment, physiology, and perhaps the method used to calculate it.

Estimated weight-specific ingestion rates were determined for the 10 species from the relationship $I = G/K_1$. For these species there is a good relationship between ingestion rate (I) and growth rate (G) (Fig. 5).

$$I = 0.1203 + 2.8691\,G$$

$$r^2 = 0.80 \qquad S_b = 0.5140. \tag{5}$$

There was no detectable relationship between ingestion and temperature for these 10 species because of the highly variable growth rates and growth efficiencies that were reported. However, given the relationship between G and T (Equation (1)) and the mean value for K_1, an expression describing a general relationship between I and T for marine fish larvae was derived.

$$I = G/K_1 \qquad I = (-0.0036 + 0.0094\,T)/0.29,$$

yielding

$$I = -0.0125 + 0.0326\,T. \tag{6}$$

Thus, to attain the expected growth rate, ingestion must increase with temperature. A threefold increase in weight-specific ingestion rate is required to meet the demands of expected growth at 30°C compared with that needed at 10°C. The result demonstrates that tropical fish larvae or those living at high summer temperatures must ingest relatively large amounts

TABLE 5.—Gross growth efficiencies (K_1) of marine fish larvae from laboratory experiments.

Species	Temperature (°C) Range	Temperature (°C) Midpoint	Mortality coefficient (Z) Range	Mortality coefficient (Z) Midpoint	References
Clupea harengus CH	7.0–9.0	8.0	<0.10–0.62	0.360	Checkley 1984; Kiorboe and Munk 1986; Kiorboe et al. 1987
Anchoa mitchilli AM	26.0	26.0	[1]0.11–0.32	0.215	Houde and Schekter 1981, 1983
Engraulis mordax EM	15.5	15.5	0.24–0.46	0.350	Theilacker 1987
Dicentrarchus labrax DL	18.0–19.0	18.5	0.26–0.57	0.415	Barahona-Fernandez and Girin 1977
Morone saxatilis MS	18.0–21.0	19.5	0.14–0.32	0.230	Eldridge et al. 1982; Chesney 1986; Tuncer 1988
Archosargus rhomboidalis AR	23.0–29.0	26.0	[1]0.21–0.41	0.310	Stepien 1976; Houde and Schekter 1981, 1983
Scomber japonicus SJ	17.0–22.0	19.5	0.20–0.44	0.320	Hunter and Kimbrell 1980
Paralichthys dentatus PD	18.0	18.0	0.05–0.24	0.145	Buckley and Dillman 1982
Pseudopleuronectes americanus PA	6.0–8.0	7.0	0.05–0.33	0.190	Laurence 1977; Cetta and Capuzzo 1982
Achirus lineatus AL	28.0	28.0	[1]0.13–0.52	0.325	Houde and Schekter 1981, 1983

[1]The highest values reported by Houde and Schekter (1981) were not included here, based on their note that these values were in error.

of food to grow at their observed, average rates. Because it depends on the relationship between growth rate and temperature, the Q_{10} for ingestion rate in the 5°–30°C range is 2.11, the same as that calculated for growth rate.

From the estimates of weight-specific ingestion (Table 6), the numbers of food organisms were calculated that would satisfy the growth requirements of first-feeding larvae of the 10 species. The number of required prey is directly proportional to growth rate and to W_0, the initial dry weight of a larva, and is inversely propor-

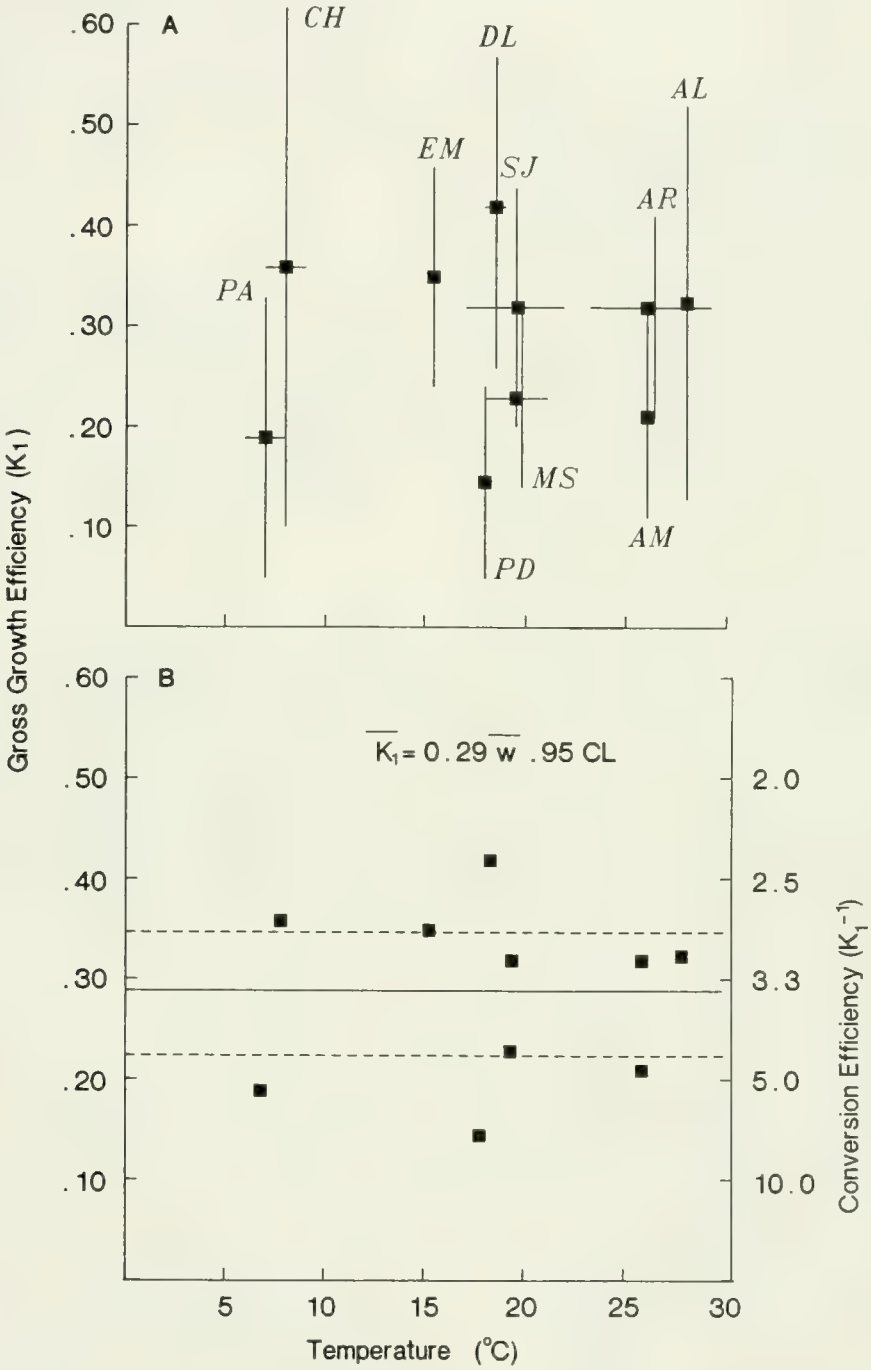

FIGURE 4.—Gross growth efficiency (K_1) and conversion efficiency (K_1^{-1}) of marine fish larvae in relation to temperature (T). A. Ranges and midpoints of K_1 and T values. Data, letters designating species and references are from Table 5. B. Mean K_1 and 0.95 confidence limits from the attempt to regress midpoint K_1 on midpoint T. There was no significant regression of K_1 on T.

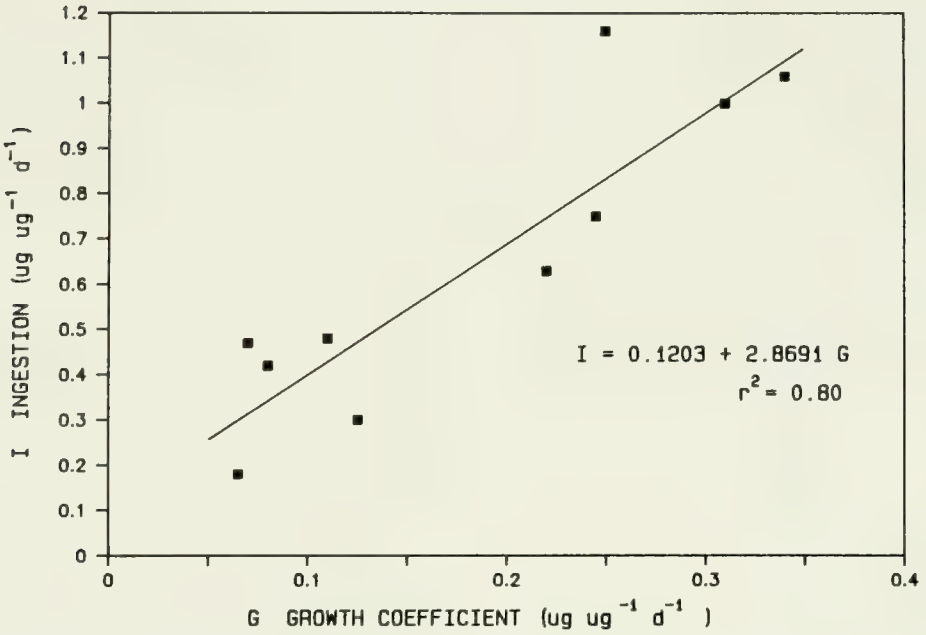

FIGURE 5.—Weight-specific ingestion rates (I) of marine fish larvae in relation to weight-specific growth coefficient (G). Data derived from Tables 2 and 5.

TABLE 6.—Estimated numbers of 0.25 μg dry weight food particles required by first-feeding marine fish larvae to meet their reported mean growth rates. Required total ingestion and weight-specific ingestion (i.e., number of particles per μg of growth) are given. Estimates were calculated from the G and K_1 values derived from published literature (see Tables 2, 4).

Species	Midpoint temperature (°C)	Midpoint G (μg μg^{-1} d^{-1})	Midpoint K_1	Initial larval weight (μg)	Daily weight increment (μg)	Number of 0.25 μg particles required (d^{-1})	Weight-specific ingestion (number μg^{-1}) d^{-1}
Clupea harengus CH	11.5	0.065	0.360	80	5.2	57.8	11.12
Anchoa mitchilli AM	27.0	0.250	0.215	10	2.5	46.5	18.60
Engraulis mordax EM	14.5	0.220	0.350	20	4.4	50.3	11.44
Dicentrarchus labrax DL	16.5	0.125	0.415	90	11.3	108.9	9.64
Morone saxatilis MS	17.0	0.110	0.230	200	22.0	382.8	17.40
Archosargus rhomboidalis AR	26.0	0.310	0.310	10	3.1	40.1	12.92
Scomber japonicus SJ	19.5	0.340	0.320	30	10.2	127.7	12.52
Paralichthys dentatus PD	18.0	0.070	0.145	~50	3.5	96.6	27.59
Pseudopleuronectes americanus PA	6.0	0.080	0.190	10	0.8	16.8	21.05
Achirus lineatus AL	28.0	0.245	0.325	10	2.5	30.2	12.32

tional to gross growth efficiency. Required prey of 0.25 μg dry weight (the approximate weight of a 100–200 μm width copepod nauplius) varied more than twentyfold, ranging from 17 to 383 d^{-1} among the 10 species (Table 6). Marine fish larvae must ingest 15.3 prey of 0.25 μg dry weight (15.3 ± 3.9 with 0.95 confidence limit) to attain a 1 μg increase in dry weight. To the extent that 0.25 μg either underestimates or overestimates the mean weight of a prey for a species of fish larva, the required numbers of prey were either overestimated or underestimated.

Metabolism

Weight-specific oxygen uptakes of feeding-stage larvae of 13 species ranged from 0.3 to 44.9 μL/mg/h and increased with temperature. All of the values, except those for haddock, *Melanogrammus aeglefinus*, which were considered outliers, were used in the regression describing the relationship between oxygen uptake (Q_{O_2}) and temperature (T) (Table 7; Fig. 6).

$$Q_{O_2} = 2.3973 + 0.2187\ T$$

$$r^2 = 0.39 \qquad S_b = 0.0870. \qquad (7)$$

The relationship was significant ($P = 0.025$), but the fit was not as good as those of the other regressions. In the 5°–30°C range, Q_{10} was 1.46, a value lower than that calculated for growth and ingestion rates.

After rearranging and substituting Equation (1) into Equation (7), an expression between oxygen uptake (Q_{O_2}) and growth rate (G) was derived.

$$Q_{O_2} = 2.2472 + 23.5000\ G \qquad (8)$$

From this relationship it can be seen that for growth rate in the sixfold range of 0.05–0.30, oxygen uptake varied only by a factor of 2.7.

Energy Budgets

There were substantial effects of temperature on the calculated energy budgets. Weight-specific ingestion rate increased threefold in the 10C°–30°C range (Table 8). Numbers of calories increased in all budget components as temperature increased. The relative contributions of each budget component show that growth remained constant, a consequence of gross growth efficiency being constant over all temperatures, and that relative metabolism declined at higher temperatures. Assimilation efficiencies declined from 77.1% at 10°C to 59.8% at 30°C. Net growth efficiencies, K_2, increased from 37.2% at 10°C to 48.1% at 30°C. Fecal energy increased twofold, from 22.9% at 10°C to 40.2% at 30°C.

DISCUSSION

Predicted growth and mortality rates of marine fish larvae increase by approximately 0.01 per degree in temperature, implying large differences in developmental times and daily probabilities of death in larvae that are hatched in either warm or cold seas. The very high growth and mortality rates at the high temperatures in tropical latitudes indicate fast turnovers of larval populations compared with the longer turnover times expected in temperate seas. In reviewing mortality of marine organisms in relation to their size, Peterson and Wroblewski (1984) and McGurk (1986) noted the exceptionally high mortality rates of marine fish eggs and larvae and discussed some probable reasons and consequences. McGurk (1986) believed that patchiness and susceptibility to predation explained the relatively high rates of mortality. The analyses presented here demonstrate that the rates not only are high but that they vary predictably with temperature. Based on the species that are represented, the results are presumed to represent a latitudinal trend as well as to be seasonally significant. More than fourfold differences in the expected mortality rates of marine fish larvae can be attributed to environmental temperature, without considering effects of larval size, in the 5°–30°C range. Expected weight-specific growth rates of fish larvae also were demonstrated to be six times higher at temperatures in tropical seas (30°C) than at temperatures in cold seas (5°C).

A consequence of declining temperature is an exponential increase in predicted larval stage duration (Fig. 2). Stage durations for larvae that develop at ≤8°C exceed 100 days, while larvae that develop at the 25°–30°C temperatures in tropical seas, metamorphose in ≤30 days. More importantly, there is a relatively large increase in its potential variability as stage duration increases. The highest variability in growth rate is observed in species that develop at high temperature (Fig. 1), but the highest variability in stage duration is observed at low temperature. Consequently, small changes in growth rate can

TABLE 7.—Weight-specific oxygen consumptions (Q_{O_2}) of marine fish larvae. Values given are for feeding-stage larvae. Some Q_{O_2} values were calculated from oxygen uptake on larval weight regressions if these were given by the authors.

Species	Temperature (°C) Range	Midpoint	Q_{O_2} (μL mg^{-1} h^{-1}) Range	Midpoint	References
Clupea harengus CH	5.0–18.0	11.5	0.30–5.00	2.65	Holliday et al. 1964; DeSilva and Tytler 1973; Eldridge et al. 1977; Almatar 1984; Kiorboe et al. 1987
Sardinops sagax SS	14.0	14.0	1.30–2.70	2.00	Lasker and Theilacker 1962
Anchoa mitchilli AM	26.0	26.0	4.00–8.20	6.10	Houde and Schekter 1983
Engraulis mordax EM	16.0–17.0	16.5	3.16–7.74	5.45	Theilacker and Dorsey 1980; Theilacker 1987
Gadus morhua GM	4.0–10.0	7.0	1.00–8.87	4.95	Laurence 1978; Davenport and Lonning 1980; Solberg and Tilseth 1984
Melanogrammus aegleinus MA	4.0–9.0	6.5	4.90–44.90	[1]24.90	Laurence 1978
Merluccius productus MP	8.0–15.0	11.5	4.50–12.10	8.30	Bailey 1982
Morone saxatilis MS	18.0	18.0	3.60–7.60	5.60	Eldridge et al. 1982
Archosargue rhomboidalis AR	26.0	26.0	5.6–11.03	8.32	Houde and Schekter 1983
Scomber japonicus SJ	18.0–22.0	20.0	6.10–11.4	8.75	Hunter and Kimbrell 1980
Pleuronectes platessa PP	5.0–18.0	11.5	1.10–5.98	3.54	DeSilva and Tytler 1973; Almatar 1984
Pseudopleuronectes americanus PA	2.0–8.0	5.0	1.80–8.00	4.90	Laurence 1975; Cetta and Capuzzo 1982
Achirus lineatus AL	28.0	28.0	2.00–19.70	10.85	Houde and Schekter 1983

[1]These values were calculated from the respiration on larval weight regressions in Laurence (1978). The values seem inordinately high and were not used in deriving the Eq. 7 relationship between Q_{O_2} and temperature.

TABLE 8.—Average energy budgets of first-feeding marine fish larvae derived from the growth, metabolism and growth efficiency data in the published literature. Absolute and relative (i.e. percent) budgets are presented for 10°, 20°, and 30°C. I = ingestion and G = growth (both assumed to have equivalencies of 5,000 cal g^{-1}). M = metabolism (converted from Q_{O_2} to energy units by the oxycalorific equivalent of 0.00463 cal μL^{-1} O_2). F = feces (calculated by difference). Budget is $I = G + M + F$. $K_1 = G/I$ $K_2 = G/(G + M)$ $A = (G + M)/I$.

Temperature (°C)	Absolute budget (cal μg^{-1} d^{-1})	Relative budget (%)	K_1	K_2	A
10	0.00157 = 0.00045 + 0.00076 + 0.00036	100 = 28.7 + 48.4 + 22.9	0.287	0.372	0.771
20	0.00320 = 0.00092 + 0.00113 + 0.00115	100 = 28.7 + 35.3 + 36.0	0.287	0.449	0.641
30	0.00483 = 0.00139 + 0.00150 + 0.00194	100 = 28.7 + 31.1 + 40.2	0.287	0.481	0.598

induce large changes in stage duration when temperature is low, a result that may significantly affect the recruitment process.

Within a species gross growth efficiency varies inversely in relation to ingestion (Checkley 1984; Kiorboe et al. 1987), and it probably varies in relation to other environmental factors as well. But, on average, the calculated gross growth efficiency for marine fish larvae equaled 0.29 ± 0.06 and there is no apparent relationship to temperature. It is noteworthy that the mean gross growth efficiency calculated for marine fish larvae is identical to that reported for juvenile carnivorous fishes (Brett and Groves 1979). Because growth efficiency does not increase, larvae at high temperatures must attain fast growth through increased food consumption. The derived relationship between ingestion and temperature indicates that ingestion must increase nearly threefold to support average growth at 30°C compared to 10°C.

Values of gross growth efficiency exceeding

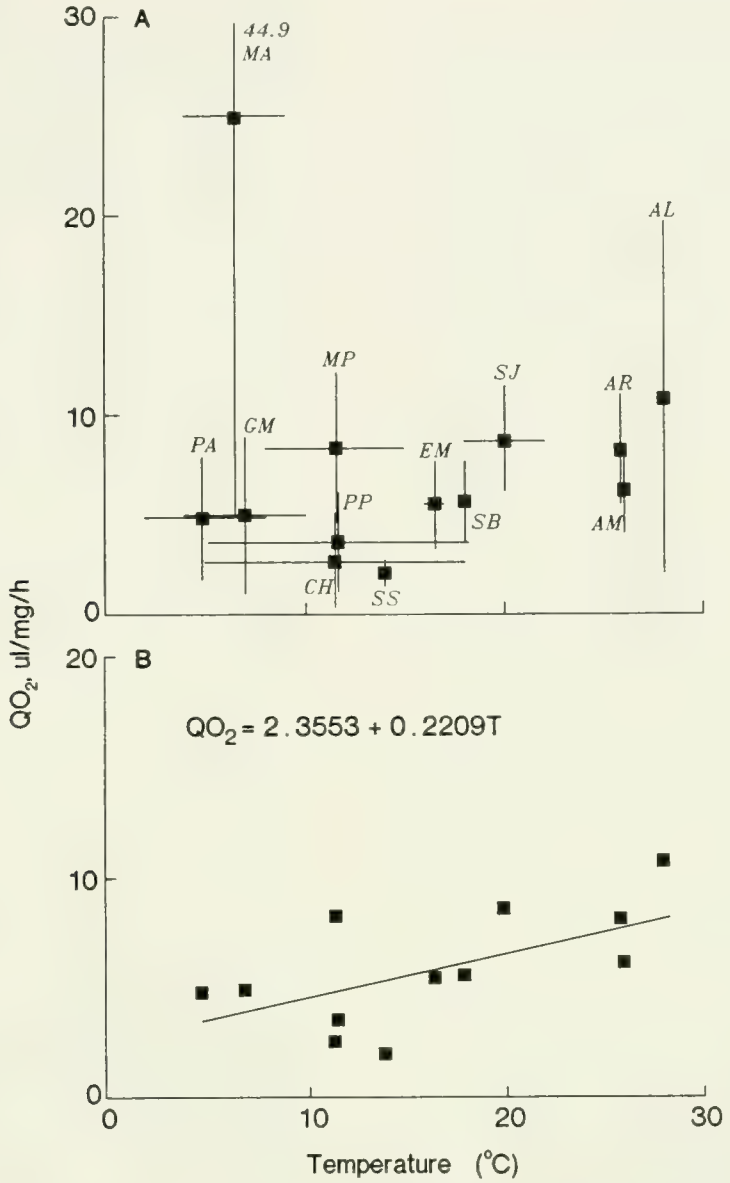

FIGURE 6.—Weight-specific oxygen uptake (Q_{O_2}) of marine fish larvae in relation to temperature (T). A. Ranges and midpoints of Q_{O_2} and T values. Data, letters designating species and references are from Table 7. B. Regression relationship of midpoint Q_{O_2} on midpoint T. The data point for haddock (i.e., MA) is not included in the regression.

0.50 for marine fish larvae have been reported, e.g., in *C. harengus* (Checkley 1984; Kiorboe et al. 1987). Kiorboe et al. argued that herring, and possibly fish larvae in general, may be operating near peak growth and assimilation efficiency, but most published estimates indicate that larvae are no more efficient than juvenile fishes or other fast-growing animals. Boehlert and Yoklavich (1984) obtained assimilation efficiencies for Pacific herring, *C. harengus pallasi*, larvae in the range of 40–60%. This implies that gross growth efficiency was considerably lower, because assimilation efficiency includes energy of metabolism as well as growth.

Weight-specific oxygen consumption increases slowly in relation to temperature compared to the observed increase in growth rate. Rombough (1988) noted that the Q_{10} for oxygen uptake by individual species of fish eggs and larvae ranges from 1.5 to 4.9, averaging 3.0. These values are considerably higher than the Q_{10} of 1.46 estimated here as the among species temperature (presumed latitudinal) effect on marine fish larvae. Still, fish larvae in warm seas have a

higher oxygen demand than larvae in colder seas. If gross growth efficiency is constant in relation to temperature, then assimilation efficiency should decline as temperature increases, while net growth efficiency should increase. Based on the calculated energy budgets at 10°C, 20°, and 30°C (Table 8), predicted assimilation efficiency declined from 77.1% at 10°C to 59.8% at 30°C. Average assimilation efficiencies of larval fish generally are thought to be similar to or less than the 80% mean assimilation efficiency of juveniles (Brett and Groves 1979; Govoni et al. 1986). Net growth efficiency increased from 37.2% at 10°C to 48.1% at 30°C. The range of predicted values of larval net gross efficiency lies just above the 36% mean value reported for juvenile fishes (Brett and Groves 1979). Recently, Wieser et al. (1988) estimated the net growth efficiency for larvae of the freshwater *Rutilus rutilus* and indicated that it was high and independent of temperature in the 15°–20°C range. Inspection of their table 4 data indicates that the net growth efficiency did in fact increase by approximately 4% in the 5°C range of their experiments, a percentage similar to that predicted from the energy budget analysis for marine fish larvae.

The mean assimilation efficiency for marine fish larvae declined as temperature increased. There also is good evidence that both assimilation and gross growth efficiency of an individual species decline at high ingestion rates (Houde and Schekter 1981; Checkley 1984; Boehlert and Yoklavich 1984; Kiorboe et al. 1987; Theilacker 1987). The ability of larvae to capture prey, the feeding conditions, and environmental factors all affect assimilation and growth, as well as their variability. Nevertheless, the efficiencies predicted here and their relationships to temperature still are believed to describe important latitudinal effects.

Despite expected high mortality rates, average survivorship of larval cohorts at tropical temperatures was predicted to exceed that of cohorts at high latitude temperatures. This result is a consequence of the high growth rates and the relatively short stage durations that tropical larvae experience. While net survivorship to metamorphosis in tropical systems may be relatively high, the daily probability of death also is high. Unless larval food abundance is higher or tropical larvae are better able than high latitude larvae to feed on scarce prey, neither of which has been demonstrated, starvation or other "critical period" mortalities (sensu Hjort 1914) may be more probable in the tropics. Cohort survivorship is sensitive to small changes in mortality and growth rates in either tropical or high latitude systems. But, larval cohorts developing in high latitudes are likely to suffer proportionally greater declines from small decreases in growth rates or increases in mortality rates, a consequence of their extended larval stage duration. If even weak or sporadic density-dependent growth or mortality operates in the larval stage (Rothschild 1986), its effect could be substantial in high latitudes where the larval stage is long.

Based on this analysis, starvation of first-feeding larvae is hypothesized to be more likely in warm seas because of their relatively great ingestion requirement combined with low assimilation efficiency. If it were possible for fish larvae to live on a maintenance diet, they would face less risk of food-limitation. But, in laboratory experiments it has been observed that slow-growing larvae are less likely to survive (Laurence 1977; Houde and Schekter 1980, 1981). Estimates here indicate that approximately 15 food particles of 0.25 μg dry weight are required to produce 1 μg dry weight of larval growth. Tropical fish larvae that are growing 2–3 times as fast as larvae from cold seas, and which also have an elevated metabolism, must consume nearly three times as much prey to achieve average growth at ambient temperatures.

Average relationships reported here indicate that larval mortality rates exceed weight-specific growth rates. Morse (1989) also has examined the relationship among growth, mortality, and temperature for 26 species of North Atlantic fish larvae. He found that both growth rates and mortality rates increased with temperature. He concluded that the ratio of mortality rates to growth rates is less than 1.0 for most of those species, and suggested that, when ratios exceeded 1.0, gear avoidance is the possible cause. In my analysis I have accepted the possibility that mortality rates may exceed growth rates for teleost larvae, implying that there is a loss of biomass between the egg stage and metamorphosis in most species. The ratio of mortality rates to growth rates, based on the regression coefficients in the mortality rates on temperature and growth rates on temperature regressions is 1.31. Morse (1989) concluded that if larval growth rate is known, then mortality rates can be predicted because the two rates are correlated. This conclusion supports the obser-

vation that mortality rates potentially can be derived from relatively easy to obtain information on larval growth rate and its variability (Houde 1987). Before such estimates are possible, it will be necessary to explicitly determine the growth rates and mortality rates of many species to establish how reliable this approach might be.

Differences in spawning strategies of marine fishes may have evolved as a consequence of the different constraints on growth and survival of larvae from high and low latitudes. The constraints for low-latitude larvae, i.e., high mortality rates, high growth rates with attendant short stage duration, and required high ingestion, suggest that few larval cohorts will find the necessary local conditions conducive for growth and survival. In most cases cohorts will starve or be eaten. It is hypothesized that protracted spawning, serial spawning and frequent batch production of eggs, a common strategy in the tropics, will insure that some larval cohorts hatch during those brief periods when conditions favor the high growth rates that promote survival. In high latitudes, where spawning often is temporally and spatially confined, larvae have different constraints. There, both mortality and growth rates tend to be low, ingestion is relatively low, but stage duration is long and potentially very variable. Under such circumstances small changes in either mortality rates or growth rates can have major impacts on recruitment potential (Shepherd and Cushing 1980; Houde 1987). And, long larval stage durations also provide ample time for density-dependent mechanisms to develop which may regulate abundance and dampen fluctuations in stocks that originated from one or a few batch spawnings that occurred during a brief time. Under these conditions the timing of spawning (Cushing 1975) and the selection of favorable spawning sites (Iles and Sinclair 1982) by adults are critical to the recruitment success of a cohort.

Although density-dependent regulation in early life often is assumed, there is relatively little evidence that it does in fact play a major role in the egg and larval stage. Jones (1973), Cushing and Harris (1973), Ware (1975), and Shepherd and Cushing (1980) have modeled the recruitment process, demonstrating how density-dependent mortality and/or growth can regulate abundance. They have argued that regulation may be most effective in the larval stage. In support of those arguments, Savoy and Crecco (1988) have demonstrated that density-dependent mortality during the egg and larval stage may play a significant role in the regulation of anadromous American shad, *Alosa sapidissima*, populations. Based on analyses of larval life history characteristics reported here, if density-dependent regulation is significant, it seems more likely to be effective in high latitudes than in tropical seas. The long stage duration and its potential variability, caused by varying temperature or food availability, may promote competition or allow predators to aggregate, favoring density-dependent control. In contrast, because larval stage durations in tropical seas are short and less variable, the probabilities of competitive or predator-mediated, density-dependent effects seem less likely.

The production of multiple cohorts during protracted spawning by tropical fishes and by many summer spawners in higher latitudes is a bet-hedging strategy that will allow some daily-produced cohorts to experience conditions favorable for survival. Lambert (1984) and Lambert and Ware (1984) have proposed that single batch, demersal spawners in high latitudes (e.g., herring and capelin, *Mallotus villosus)* are more likely to produce easily discernible cohorts of larvae than are summer-spawning pelagic species (e.g., Atlantic mackerel, *Scomber scombrus*, and white hake, *Urophycis tenuis*) in the same region because the demersal spawners are characterized by waves of females that deposit eggs at discrete time intervals. They argued that, in the cases of herring and capelin, widely spaced cohort production represented bet-hedging by reducing potential intraspecific competition among larvae and by assuring that cohorts of prey would develop with cohorts of fish larvae (Jones 1973; Jones and Hall 1974). Lambert and Ware (1984) believed that Atlantic mackerel and white hake females spawned every 2–3 days and that spawning in such species would appear to be continuous during their summer spawning season. In agreement with that argument, it is hypothesized here that teleost stocks spawning at high temperatures are more likely to produce daily cohorts of eggs than are those stocks spawning at low temperatures because the larvae of warm-water stocks have short stage durations and are constrained by the necessity for high growth and by their high mortality rates. This point is supported by Lambert and Ware's (1984) figure 4, in which they show that when larval growth rates are high, as they are in the tropics and in many high-latitude summer spawners, the predicted time period between

cohorts is reduced to only a few days. Under such conditions tropical species may spawn frequently for long periods (Clarke 1987) as a mechanism to promote recruitment success.

Several attempts have been made to develop unifying theories that explain recruitment fluctuations and regulation, including the match-mismatch hypothesis (Cushing 1975), the stable ocean hypothesis (Lasker 1978; 1981), and the larval retention hypothesis (Iles and Sinclair 1982). None of these is entirely satisfying, given the diverse nature of teleost fishes and the environments in which they live. Miller et al. (1988) have demonstrated that interspecific variation in larval size is a strong determinant of growth rate and a predictor of starvation-induced mortality. Hunter (1981) also recognized that larvae could be classified by their relative first-feeding abilities as judged by mouth size and general morphology. Miller et al. (1988) and Hunter (1981) have demonstrated that larvae can be categorized by their morphology as starvation-prone or not. Here, it is demonstrated that temperature, and by implication latitude, exercises a strong influence on the energetics, growth, and mortality rates of marine fish larvae. Furthermore, it is proposed that these traits have favored selection of spawning strategies that have evolved in warm and cold seas.

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Comparison of the Mortality Rates of Pacific Sardine, *Sardinops sagax*, and Peruvian anchovy, *Engraulis ringens*, Eggs off Peru[1]

Paul E. Smith, Haydee Santander, and Juergen Alheit

ABSTRACT: Egg production and mortality rates were estimated for populations of Pacific sardine, *Sardinops sagax*, and Peruvian anchovy, *Engraulis ringens*, off north and central Peru for August to September 1981. Peruvian anchovy spawned in the entire inshore region, principally within 56 km (30 nmi) of the coast. The Pacific sardine spawned extensively in the northern and southern inshore regions but not in the central region. While spawning of the two species coincided at the regional scale, at the sample scale, the occurrence of eggs of the two species was statistically independent. The egg production rate of Peruvian anchovy was about double that of sardine. The mortality rate of Pacific sardine eggs was much higher than that of Peruvian anchovy. The egg mortality rates of Peruvian anchovy and Pacific sardine were unchanged at stations where Pacific sardine and Peruvian anchovy eggs occurred together, relative to where the two species' eggs occurred separately. Results of this study are used to evaluate cannibalism as a population limiting mechanism. Cannibalism accounts for about 30% of egg mortality in anchovy. Because of the schooling habit of sardines and anchovies, cannibalism, though large-scale, may not vary enough with population size to explain variations in recruitment.

In their review of clupeoid biology, Blaxter and Hunter (1982) emphasized the need to estimate instantaneous rates as the "only way to establish a satisfactory linkage between the fish and their environment." These instantaneous rates include production of spawn (Lasker 1985) and mortality rate of the eggs and larvae. Predation is thought to be an important cause of mortality, and one form of predation, cannibalism, has been proposed as a mechanism for establishing an upper limit to population density (Ricker 1954; Hunter and Kimbrell 1980; MacCall 1980; Alheit 1987; Pauly and Soriano 1987) of filter-feeding, pelagic spawning, schooling coastal pelagic fishes.

MacCall (1983) has described abundance as a composite of population density and geographic extent: northern anchovy, *Engraulis mordax*, appears to have a central area where density-dependent processes have their greatest effect on local density and a peripheral area where density-dependent processes are less important. Reductions of density in the central area result in contractions of the population to the central area for Pacific sardines, *Sardinops sagax*, (Murphy 1966) and northern anchovy (MacCall 1980). Off California both sardines and anchovy contract to the same area (Ahlstrom 1967).

Microstructure in the sea plays an important role in interaction of predator and prey (Lasker and Smith 1977) at the embryonic and larval stages (Smith 1973; Vlymen 1977; Theilacker 1987). There may also be rapid changes in the microstructure due to dispersal (Smith 1973; Smith and Hewitt 1985b). McGurk (1987) has proposed that small-scale pattern may make mortality rates proportional to patchiness rather than inversely proportional as originally suggested by Brock and Riffenburgh (1960).

Subsequent variations in recruitment may be caused by environmental influences on first-feeding larvae (Hjort 1926; Lasker 1975, 1978, 1981; Peterman and Bradford 1987), and recruitment is regulated by the interaction of growth and mortality rates of juveniles (Shepherd and Cushing 1979; Smith 1985; Butler 1987). Peterman et al. (1988) demonstrated that in a selected subset of years there was no relationship be-

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tween the abundance of northern anchovy larvae off California at 20 days of age and the recruitment at age 1. It had previously been shown that, for a shorter time series in the same habitat, Pacific sardine recruitment at two years old varied 15-fold, while the egg abundance in the year of origin for the same years varied only 3-fold (Smith 1978).

A major barrier to estimating egg mortality in pelagic schooling fish is the tendency of these fish to aggregate closely for external fertilization of spawn (Leong in press), presumably to conserve sperm and ensure high fertilization rates. The eggs are subsequently dispersed by turbulent diffusion (Smith 1973; Smith and Hewitt 1985a). Schooled spawning, with its spatially intense pattern, imposes a high sample variance on the younger eggs, and dispersal reduces the sample variance with time (Smith and Hewitt 1985a).

Precise estimation of survival and egg production rates requires large numbers of samples. The intensity of patchiness is indicated by the maximum values for egg counts. Smith (1973) observed that the concentration of Pacific sardine eggs off California was a maximum of 3,100 eggs/m^2, and Hunter (1980) observed that a concentration of 1 d old northern anchovy eggs was 4,600 per m^2. Walsh et al. (1980) reported the results of sample analyses of Peruvian anchovy eggs along the Peruvian coast. From five samples at lat. 10°S and seven samples at 15°S, they found a maximum value of 11,500 Peruvian anchovy eggs/m^2, and they also found Peruvian anchovy larvae at 100 and 200 per m^2. Santander et al. (1982) reported on Peruvian anchovy and Pacific sardine off Peru. For Peruvian anchovy, they found a maximum egg concentration of 107,376 eggs/m^2 (all ages). This count was from the largest of 911 ichthyoplankton tows with Peruvian anchovy eggs out of 4,028 Hensen net samples between 1966 and 1979. For Pacific sardine off Peru, the maximum egg concentration was 58,500 eggs/m^2 (H. Santander[2]). This count was from the same set of 4,028 tows.

Pacific sardine spawning off Peru has been essentially stable between 1978 and 1981 (Santander 1981). What are the implications for selection of spawning sites for the two pelagic spawners? Do the two species partition the environment into separate spawning areas or do they concentrate on oceanic sites favorable to both? What are the relative rates of egg production and mortality where they co-occur?

In this paper we describe regional and interspecific differences in egg production and mortality off Peru. The Peruvian anchovy data used for this paper have already been used for estimating egg production of the Peruvian anchovy population off north and central Peru (Santander et al. 1984). The Pacific sardine egg data off Peru are adequate for determining egg production per unit area, but contemporaneous adult reproduction rates are lacking; thus, sardine adult biomass has not been estimated.

METHODS

Cruise plan, sampling methods, laboratory methods, and data analysis have been described fully by Santander et al. (1984; an English version can be obtained from the author J. Alheit). Only a brief account of these methods is presented here.

The objective of the investigation was to encompass the Peruvian anchovy and Pacific sardine spawning grounds off northern and central Peru with an intensive grid of ichthyoplankton stations. The survey extended from Pisco (lat. 14°S) in the south to Punta Falsa (6°S) in the north. The background, a computer program for distributing the stations, and other technical details of the cruise plan are described in Smith et al. (1983). The sampling stations were distributed on transects perpendicular to the coastline. The inshore spacing of transects was 10 nmi. Thirty-five transects extended 30 miles offshore and 18 transects extended 90 miles offshore. On all transects the sampling stations were three miles apart. The total number of stations was 925. The area under investigation was subsequently divided into nine regions for some aspects of the analysis (Fig. 1).

Eggs were sampled with the CalVET net (CalCOFI vertical egg tow; Smith et al. 1985). Its mesh size was 333 μm, and its mouth area was 0.05 m^2. The net was towed vertically from a 70 m depth to the surface within 1 minute. The net filtered 3.5 m^3 of water.

Following sorting, the eggs were aged according to their developmental stage, the surface water temperature, and the time of day when the sample was collected. The following is a brief summary of the method for determining Peruvian anchovy egg production; a complete description of these techniques for northern anchovy is found in Picquelle and Stauffer (1985).

[2]H. Santander, Instituto del Mar del Peru, Apartado 22, Callao, Peru, unpubl. data.

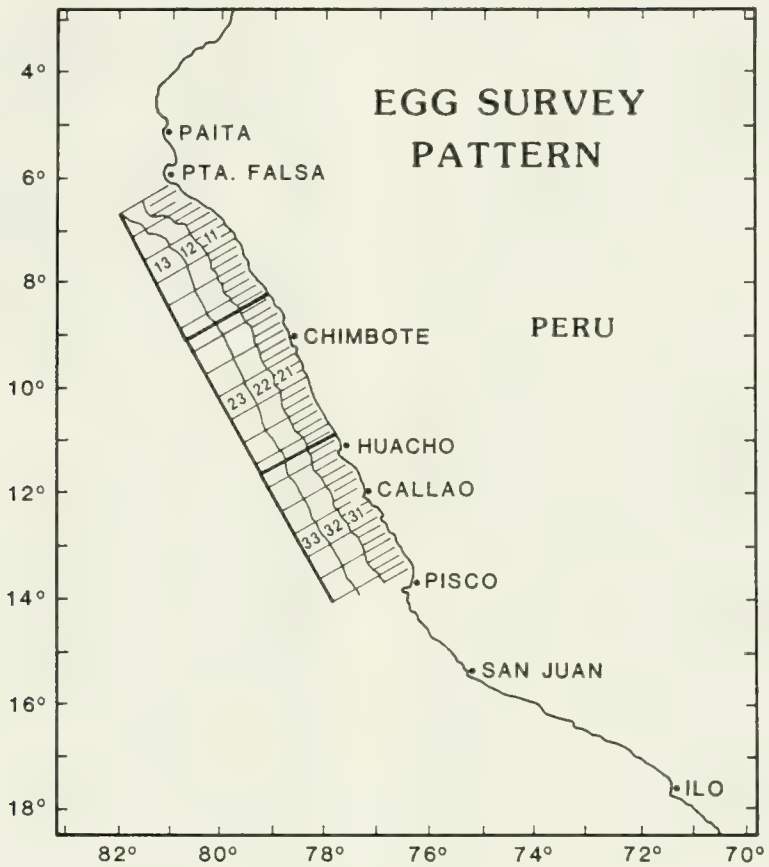

FIGURE 1.—Coastline of Peru and egg survey stations and statistical regions. Egg sampling stations are 3 miles apart in the cross-shelf plane. Regions for statistical summaries are coded. The first digit of each number refers to the north "1", central "2", or south "3" sectors of the coast. The second number refers to the inshore "1", offshore "2", or seaward "3" regions of each sector. In text, codes referred to as IMAR11, IMAR12, etc. to distinguish the codes from numbers. Original station positions and equations for plotting are in Smith et. al. (1983).

Anchovy and sardine eggs were grouped in 12 h intervals. Newly spawned eggs collected during the spawning interval and older eggs collected during hatching were eliminated from the calculations. The remaining egg counts were regressed on age to fit a mortality function of the egg data. The daily egg production was then estimated by zero intercept of the exponential mortality function. The following exponential model can be fit to the egg data by the nonlinear, least squares regression (Stauffer and Picquelle 1980[3]):

$$P_0 = P_i\, e^{-zt}$$

where P_0 = daily egg production;
P_i = number of eggs of age t_i sampled during the time interval t_i, t_{i+1};
t = time elapsed between spawning and the ith time interval; and,
Z = instantaneous daily rate of egg mortality.

The P_0 is the intercept of the exponential curve. The model assumes that all eggs are spawned and fertilized at an instant, that the eggs have a constant rate of mortality, and that the sampling was representative and includes all areas where eggs may be found.

RESULTS

Peruvian anchovy and Pacific sardine co-occur along the north and central coast of Peru

[3]Stauffer, G. D., and S. J. Picquelle. 1980. Estimates of the 1980 spawning biomass of the central subpopulation of northern anchovy. U.S. Dep. Commer., NOAA, NMFS SWFC Adm. Rep. LJ-80-09, 41 p.

(Santander 1981). In 1981, the Peruvian anchovy egg distribution was essentially continuous near the coast, with some extension offshore to 30 miles offshore of Chimbote (Fig. 2). In contrast, the Pacific sardine eggs occurred in two groups separated by about 120 nmi between Huacho and Chimbote. The Pacific sardine eggs extended farther offshore than Peruvian anchovy eggs and were not as abundant in the nearshore stations.

Of the 925 samples that were taken (Santander et al. 1984), 575 came from the inshore regions IMAR11, IMAR21, and IMAR31 (Fig. 1). Twenty-one percent of the samples in the inshore regions had both Peruvian anchovy and Pacific sardine eggs, 32% had only Peruvian anchovy eggs, 18% only Pacific sardine eggs, and 28% had neither Peruvian anchovy nor Pacific sardine eggs (Table 1).

There were fourfold fewer ½ d old Pacific sardine eggs per station in the samples with Pacific sardine eggs in the absence of Peruvian anchovy eggs as compared with Pacific sardine eggs per station when Peruvian anchovy eggs were also present (Table 2). By way of contrast, the Peruvian anchovy eggs appeared to be equally abundant, with or without Pacific sardine eggs in the sample. There appeared to be a trend of Pacific sardine egg abundance in absence of Peruvian anchovy eggs becoming proportionally less abundant with age, but the trend was mostly concealed by the high standard errors of the two categories. Of course these rates cannot be known precisely from exploratory data analysis; the absolute rates would have to result from specifically designed studies with higher precision.

TABLE 1.—Number (% in parentheses) of plankton hauls in which Peruvian anchovy, *Engraulis ringens*, and/or Peruvian sardine, *Sardinops sagax*, eggs occurred in the three inshore regions.

Region	Both anchovy and sardine	Anchovy only	Sardine only	Neither anchovy nor sardine	Total
IMAR11	51 (27)	26 (14)	65 (35)	45 (24)	187
IMAR21	34 (17)	91 (46)	18 (9)	54 (27)	197
IMAR31	36 (19)	69 (36)	22 (12)	64 (34)	191
Total	121 (21)	186 (32)	105 (18)	163 (28)	575

On a regional basis, sardine egg production was highest in the northern region (IMAR11), negligible in the central region (IMAR21), and higher in the southern region (IMAR31, Table

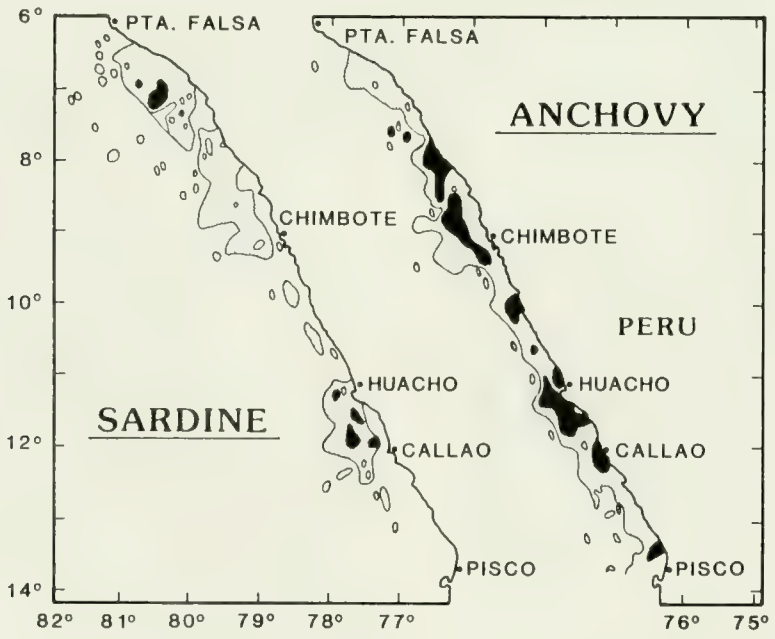

FIGURE 2.—Pacific sardine (left) and Peruvian anchovy (right) egg abundance in August to September 1981. For each species, shaded areas indicate where their eggs were taken at densities of 1–100 eggs/0.05 m^2, and black areas indicated 101 or more eggs/0.05 m^2. Peruvian anchovy data has also been mapped in units of eggs per square meter in Santander (1987, Map No. 78, p. 204).

TABLE 2.—Mean number of Peruvian anchovy, *Engraulis ringens*, and Pacific sardine, *Sardinops sagax*, eggs per station by age group. The age group code A1 refers to eggs aged in the first half of the first day after spawning; A2 refers to eggs aged in the second half of the first day; B1 refers to eggs aged in the first half of the second day; and B2 refers toe ggs aged in the second half of the second day. "All" refers to all stations where that species' eggs were present. Only the inshore regions (IMAR11, IMAR 21, IMAR31) combined were considered for estimation of these parameters. "Both" refers to those stations where eggs of both species were present. "Only" refers to stations where that species' eggs were present.

Age		Anchovy			Sardine		
group	Variable	All	Both	Only	All	Both	Only
A1	Mean	62.92	67.49	59.11	19.53	26.58	6.66
	SE	8.70	12.70	11.99	7.01	10.70	2.33
A2	Mean	22.90	36.07	16.32	6.73	12.35	2.16
	SE	3.73	9.34	2.93	1.84	3.91	0.66
B1	Mean	31.05	37.59	26.60	2.14	2.88	0.77
	SE	5.35	7.92	7.25	0.48	0.71	0.33
B2	Mean	9.36	11.15	8.46	1.32	2.62	0.23
	SE	1.31	2.37	1.58	0.57	1.24	0.12

3). Peruvian anchovy egg production was relatively even in all sectors of the inshore region. The mortality rates of both Pacific sardine and Peruvian anchovy were highest in the northern region. Pacific sardine mortality rates were higher than Peruvian anchovy mortality rates in each region.

Mortality rates of Peruvian anchovy and Pacific sardine eggs were not higher where the eggs occurred in the same samples (Table 4). Pacific sardine egg production, in areas where Pacific sardine eggs were not accompanied by Peruvian anchovy eggs in a sample, was only a third of that where the two species' eggs were found together. As in the case of abundance, Peruvian anchovy egg production and mortality rates do not appear to be related to the presence of Pacific sardine eggs in the sample.

The spatial overlap of the Pacific sardine spawning areas and Peruvian anchovy spawning areas cannot be distinguished from randomness. The probability that a 0.05 m^2 sampler will miss a Peruvian anchovy egg patch was 0.47 and for a Pacific sardine egg was 0.61 in August–September of 1981 off northern and central Peru. The joint probability of a sampler of this size missing both species' eggs as estimated from the product of the individual species' probabilities was 0.29. The measured probability of missing both species was 0.28 (Table 1). Therefore based on occurrence in a 0.05 m^2 mouth area sampler, the small-scale spatial distribution of Pacific sardine and Peruvian anchovy eggs was indistinguishable from total independence of each other.

In summary, the results of this study show that Pacific sardines and Peruvian anchovies spawned along the coast over the latitudinal extent of northern and central Peru with the preponderance of spawning within 30 nmi of the coast. The production rate of Peruvian anchovy eggs per unit area (104 eggs/0.05 m^2 d^{-1} was about double that for Pacific sardine (56 eggs/0.05 m^2 d^{-1}) and the mortality rate of Peruvian anchovy eggs ($z = -1.12$ or 67% d^{-1}) was substantially lower than that of Pacific sardine ($z = -2.12$ or 88% d^{-1}). The highest mortality rate for both species occurred in the northern region (IMAR11). For the Pacific sardine in the northern region, the instantaneous rate was -3.88 (98% d^{-1}). For the Peruvian anchovy in the north, the instantaneous rate was -2.14 or 88% d^{-1}. Mortality rates of Peru-

TABLE 3.—Regional egg production (P_0) and mortality rates (Z) of Pacific sardine and Peruvian anchovy as estimated by a nonlinear least squares procedure assuming an exponential model.

Species	Category	Production (SE) eggs/0.05 m^2/d	Mortality (SE) daily instantaneous
Sardine	IMAR11	16.6 (2.6)	3.88 (0.39)
	IMAR21	0.4 (0.1)	1.28 (0.35)
	IMAR31	8.7 (1.5)	1.47 (0.28)
Anchovy	IMAR11	22.0 (9.2)	2.14 (0.83)
	IMAR21	23.7 (6.7)	0.93 (0.36)
	IMAR31	17.0 (4.9)	0.90 (0.35)

TABLE 4.—Egg production (P_0) and mortality rates (Z) of Pacific sardine and Peruvian anchovy for all inshore regions where samples are positive for either species. "All" refers to all stations where eggs of that species were present. "Only" refers to stations which were positive for one species but the eggs of the other species were absent. "Both" refers to stations where eggs of both species were present.

Species	Category	Production (SE) eggs/0.05 m^2/d	Mortality (SE) daily instantaneous
Sardine	All	56.3 (3.2)	2.12 (0.10)
	Only	20.2 (0.4)	2.22 (0.03)
	Both	64.1 (9.2)	1.75 (0.22)
Anchovy	All	104.7 (37.2)	1.12 (0.44)
	Only	109.9 (47.0)	1.35 (0.58)
	Both	104.0 (25.5)	0.90 (0.28)

vian anchovy and Pacific sardine eggs were not higher where the eggs occurred in the same sample.

DISCUSSION

In this section we will discuss Pacific sardine and Peruvian anchovy egg production and mortality off Peru, fundamental statistical problems to be overcome in future studies, some other mechanisms of population control, and egg cannibalism and population control in pelagic spawning, schooling coastal pelagic fishes.

Pacific Sardine and Peruvian Anchovy Egg Production and Mortality

It appears that Pacific sardines and Peruvian anchovies off Peru select the same large-scale sites for egg deposition but select independently of each other at the small scale. While the eggs of both species were concentrated in the inner 30 miles of the survey pattern (Fig. 2), the probability of occurrence on a sample-by-sample basis was not demonstrably different from independent distributions for the two species (Table 1).

Where Pacific sardine and Peruvian anchovy eggs occurred together, Peruvian anchovy egg production rates were equal to those sites where Peruvian anchovy eggs occurred alone, but Pacific sardine egg production rates were higher at co-occurring sites than those sites where only Pacific sardine eggs were taken. Mortality rates where both occurred were marginally lower than where each occurred separately: this implies that the proximity of the adults of the other species does not affect the egg mortality rates. The northern region had the maximum rate of mortality for both Peruvian anchovy and Pacific sardine. The northern region had also the maximum regional rate of production for Pacific sardine, virtually equal to the Peruvian anchovy egg production rates of the other two regions (Table 3).

In all regions, the Pacific sardine mortality rate was higher than the anchovy mortality rate. Of an estimated 2,094 eggs produced/m^2 d^{-1} by Peruvian anchovy, 1,410 (67%) died on the first day. Of an estimated 1,126 eggs produced/m^2 d^{-1} by Pacific sardine, 990 (88%) died on the first day. We suggest two explanations for the cause of higher mortality rate of Pacific sardine eggs relative to Peruvian anchovy eggs in the same region: Moser[4] pointed out that the ovoid shape of the anchovy egg (0.7 × 1.4 mm) as compared with the spherical sardine egg (1.4 mm) may reduce the chance of being eaten by filter-feeders. Author H. Santander has observed that sardine eggs are more delicate to handle in the laboratory. This may mean that the integument of the sardine egg is more susceptible than the anchovy egg to physical damage by predators in the sea. Their susceptibility to damage might also explain their apparent low incidence in juvenile and adult sardine and anchovy stomachs, because broken eggs might not be detected (Santander et al. 1983).

Fundamental Statistical Problems

Errors in the estimation of the slope parameter induce errors of the same sign in the intercept parameter: for this reason there are major problems in comparing adult spawning biomass concentration derived from the intercept parameter and egg mortality rate derived from the slope parameter. Thus, for the purpose of this paper, the comparison of spawning biomass concentration and egg mortality is not reported as a result of this research. Instead, Figure 3 and Table 6 are points of discussion. The data come from a plan for stock assessment and as such are not definitive on the question of biomass concentration and egg mortality rate. The relationship is suggestive, however, and may be used to design a study of cannibalism that is not statistically confounded.

The statistical problem of patchiness (Taft 1960), encountered when estimating the abundance of fish eggs, becomes more severe when estimating production and mortality of eggs because the intensity of patchiness changes with age (Smith 1973, 1981; Smith and Hewitt 1985a, 1985b; McGurk 1987). Since the mortality estimate requires the arithmetic means (Southwood 1978), log transformation to stabilize variance is not used.

Egg production (P_0) and mortality rate (Z) are determined using the exponential mortality model (Picquelle and Stauffer 1985). It has been determined that the midpoint of spawning is at 2200 hours but samples from the spawning interval are biased (Smith and Hewitt 1985a). The intercept and mortality rate could be systematically underestimated if the actual mortality rate

[4]H. G. Moser, Southwest Fisheries Center La Jolla Laboratory, Natl. Mar. Fish. Serv., La Jolla, CA 92038, pers. commun. May 1983.

in the initial period was higher owing to an interaction between local density and mortality rate on eggs at the highest distributional densities (McGurk 1987).

The Central Limit Theorem requires independence among sample values. With the spawning of Pacific sardine and Peruvian anchovy off Peru compressed against the coast in a 30 mile band in 1981, abundance estimates from stations separated in the cross-shelf dimension at 3 mile intervals are not likely to be independent. The effect will be an underestimate of sample standard error of the mean (Table 2). The degree of the same type of error in the along-shelf plane was probably smaller because the transects are 10 nmi apart. Also the collection of sites used for the estimates of abundance of 1 and 2 d old eggs in the first half of each day (A1 and B1 in Table 2) are from different stations from those used for estimates of abundance of 1 and 2 d old eggs in the second half of each day (A2 and B2 in Table 2).

Other Mechanisms

Egg cannibalism is probably only one of several possible population controlling mechanisms in anchovies. For example, cannibalism could occur at life stages other than the egg stage. There have been recent observations, in the laboratory, of older anchovy larvae consuming younger larvae (Brownell 1985). In these observations, the larvae became more vulnerable as pigmentation formed in their eyes and integument.

Energy demands for egg production and spawning could lead to aggregations of adults where food production and, coincidentally, egg mortality are both high. That, in both Pacific sardine and Peruvian anchovy, higher rates of egg mortality and egg production occurred in the same region (IMAR11) seems to support this view. Lastly, from laboratory observations, northern anchovy larvae, only a day old, may seek and maintain position in patches of *Gymnodinium*, making these larvae vulnerable to enhanced feeding activity by many other organisms in the same patch or layer (Hunter and Thomas 1974).

Egg Cannibalism and Population Control

For the northern anchovy, *Engraulis mordax*, Peterman et al. (1988) concluded that the size of the recruited stock is not determined in the first 20 days following spawning. On the other hand, Pauly[5] concluded that egg mortality due to cannibalism by the adult stock is a primary density dependent control on recruitment in the Peruvian anchovy, *Engraulis ringens*. Smith (1985) lists three situations in which cannibalism by schooling pelagic spawners would be an effective population controlling activity: 1) directed filtering behavior on dense aggregations of eggs; 2) encounter with other schools' patches of eggs; and, 3) anchovy population switching from biting to filtering behavior.

Directed Filtering

In the first few hours after spawning, before much dispersal has taken place, directed filtering could be an important source of mortality (Smith and Hewitt 1985b; McGurk 1987). Hunter and Dorr (1982) found that adult northern anchovy filtering was induced by 5 northern anchovy eggs/L and sustained by 1 or 2 eggs/L in laboratory tanks. Given that the level of artificial feeding is higher for laboratory animals and that probably the quality of water for sensing prey is lower, these thresholds may be higher in the laboratory than in the sea. One disadvantage of this mechanism for population size control is that, because of proximity, the most likely school to encounter the newly spawned patch is the school from which the spawn was produced. Santander et al. (1983) found that Peruvian anchovy eggs < 2 hours old were overrepresented by a factor of three in the stomachs of Peruvian anchovy relative to their incidence in the sea. In a typical spawning school (Santander et al. 1984; Alheit 1985), there would be 10 times as many Peruvian anchovies feeding on eggs than females spawning eggs. While the mortality rate might be sufficient, it is difficult to seen how a change, in population size or in density over thousands of square kilometers, could materially affect a species grazing for a few hours on its own eggs over a range of a few hundred meters. This source of mortality, although large, may not be sufficiently variable with population density to control recruitment.

[5]The estimate of instananeous mortality "z" derived by Pauly (1987) is strongly biased downward at low mortality rates but should still be valid at high levels of parent stock. Daniel Pauly, International Center for Living Aquatic Resources Management, Manila, Philippines, pers. commun. March 1989.

Encounter

Incidental filtering of eggs by encounter of other schools' patches of eggs would appear to be a direct mechanism for parental control of recruitment rate and population density. If one combines the information on egg cannibalism rate by Alheit (1987) and the demographic influence on population annual fecundity reported by Pauly and Soriano (1987) (Table 5), one can see that the effective fecundity (eggs hatched after cannibalism) would be low when the stock was composed primarily of juveniles and first-year spawners.

TABLE 5.—Age-specific rates of cannibalism and egg production for anchovy.

Age (yr)	Anchovy egg production[1] (eggs/g/d)	Anchovy egg consumption[2] (eggs/g/d)	Effective fecundity (eggs/g/d)
Juveniles[3]	0.	9.3	−9.3
1	3.9	9.3	−5.4
2	9.0	9.3	−0.3
3	15.7	9.3	6.4
4	18.4	9.3	9.0

[1]Pauly and Soriano 1987
[2]Alheit 1987
[3]Ciechomski 1967

Switching

It is also possible for cannibalism to interact indirectly with population density. An indirect method for population control is evident if one considers a system where the anchovy prefer to feed by biting relatively large zooplankton and where filtering occurs only when large zooplankton are low in abundance (O'Connell 1972). Under these circumstances predation by anchovy on the major herbivores could result in a larger standing crop of phytoplankton and in increased rates of anchovy filtering (MacCall 1980). In the course of switching to a preponderance of feeding by filtering, the anchovy would inadvertently filter anchovy eggs at a higher rate.

Egg production rate was sixfold higher in Peruvian anchovy compared with northern anchovy off California (Smith and Hewitt 1985a). Of the 2,094 Peruvian anchovy eggs produced per square meter, 67% died on the first day while off California; of the 300 northern anchovy eggs produced per m^2, 22% died on the first day. While anchovy are omnivorous in both areas, phytophagy is considered more pronounced off Peru (MacCall 1980).

Pauly (1987) found that knowledge of the rate of cannibalism appears crucial for managing the Peruvian anchovy. The rate of cannibalism on eggs is admittedly high, but it may be that the variation in the rate of cannibalism is insufficient to explain the variation in the rates of recruitment. It remains to be seen if interannual differences in the relative proportion of feeding by filtration on the one hand and biting on the other hand are sufficient to explain differences in recruitment.

The difference in conclusions regarding northern anchovy egg cannibalism between Peterman et al. (1988) for California anchovy and Pauly (1987) for the Peruvian anchovy, may be due to a simple difference in population density between the two regions, California having a much lower population density than Peru. Pauly (1987) showed the relationship between population size and egg mortality: a better relationship would be between local population density and egg mortality (Csirke 1980; MacCall 1980; Ware and Tsukayama 1981).

Egg mortality rate and adult biomass density are closely related in interregional and interannual egg production assessments (Fig. 3). The relationship is surprisingly close when one considers biomass of juvenile anchovy, the biomass of other filtering fishes, particularly sardines, and the biomass of invertebrate predators have been neglected. In Table 6, one can see that northern anchovy assessment studies off California (Stauffer and Picquelle 1981; Stauffer and Charter 1982; Picquelle and Hewitt 1983, 1984; Hewitt 1985; Bindman 1986) and South Africa (Armstrong et al. 1988) differ a great deal from the assessment study reported in this paper for Peru. The median biomass density of adult anchovy was 6 g/m^2 off California between 1980 and 1985, while the median percent eggs dying each day was 16%/d. In the south Benguela Current, the mean biomass density of adult anchovy was 12 g/m^2, and the mean percentage of eggs dying per day was 22% (Armstrong et al. 1988). The median regional estimate for 1981 of biomass density of adult anchovy was 33 g/m^2 off Peru, and the egg mortality was 61% egg mortality per day. While these observations suggest cannibalism as a cause, the mortality rate of eggs may only be a consequence of generally higher populations of a wide range of other vertebrate and invertebrate predators in prime schooling fish-feeding areas.

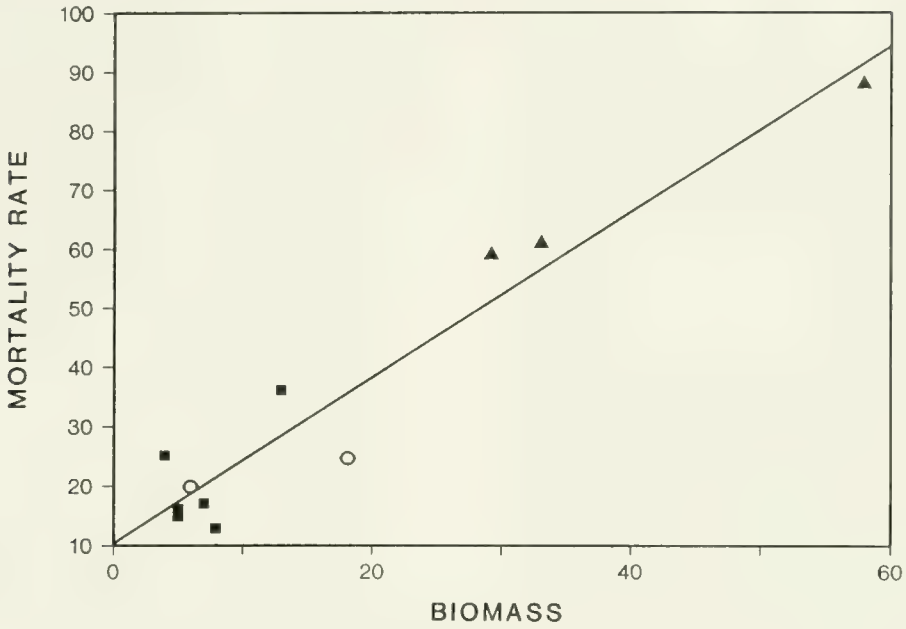

FIGURE 3.—Mortality rates in percent per day of anchovy aggs as a function of anchovy spawning biomass concentration in grams per square meter; closed triangles, Peru in nearshore regions IMAR11, IMAR21, IMAR31 (this paper); closed squares, values for the entire spawning region off California from 1980 to 1985 (Stauffer and Picquelle 1981; Stauffer and Charter 1982; Picquelle and Hewitt 1983, 1984; Hewitt 1985; Bindman 1986); and, open circles, for the entire spawning region off South Africa in 1985 and 1986 (Armstrong et. al. 1988).

TABLE 6.—Anchovy egg mortality rate and adult spawning biomass concentration in the Humboldt (*Engraulis ringens*), California (*E. mordax*), and southern Benguela (*E. capensis*) currents.

Year/region	Spawning area ($km^2 \times 10^{-3}$)	Spawning biomass (tons $\times 10^{-3}$)	Biomass concentration $g\ m^{-2}$	Egg mortality $\%\ d^{-1}$
Peru 8108				
IMAR11	7.9	460	58	88
IMAR21	12.9	420	33	61
IMAR31	11.2	320	29	59
CalCOFI 8003[1]	66.1	870	13	36
CalCOFI 8102[2]	77.5	635	8	13
CalCOFI 8202[3]	83.0	415	5	15
CalCOFI 8302[4]	94.7	652	7	17
CalCOFI 8402[5]	61.6	309	5	16
CalCOFI 8502[6]	132.2	522	4	25
Benguela				
1985[7]	107.1	614	6	20
1986[7]	109.8	2006	18	24

[1]Stauffer and Picquelle 1981.
[2]Stauffer and Charter 1982.
[3]Picquelle and Hewitt 1983.
[4]Picquelle and Hewitt 1984.
[5]Hewitt 1985.
[6]Bindman 1986.
[7]Armstrong et al. 1988.

CONCLUSION

MacCall (1980) stated that only 10% of the apparent control of northern anchovy recruitment off California may be due to stock size, with the vast majority of control arising from means that are independent of stock size. Lasker and MacCall (1983) concluded that the best measures of the stock recruitment curve are not sufficient domed for cannibalism to be a "major regulatory mechanism". Also, it appears from examination of the life stages of northern anchovy (Smith 1985, table 3) moderate reproductive failures could happen at the fecundity, embryonic, larval, and juvenile prerecruit stages, but a reproductive success of great proportions would most likely arise at the embryonic and larval stages. The size of the recruited year class will accumulate the rates of early stages, and the later the prerecruits are evaluated, the more likely the reproductive success will have been established. Peterman et al. (1988) evaluated only the first 20 days of life.

For 6 successive years (included in Peterman et al. (1988)), the interannual coefficient of variation of the spawning biomass was 35% and the interannual coefficient of variation of recruit-

ment was 104%. Only two life history parameters varied more than the spawning biomass (35%): adult density per unit area (47%) and egg mortality (38%) (Smith and Moser 1988). While cannibalism is sufficiently important as a source of egg mortality to control the size of populations like sardine and anchovy over the long term, it is unlikely that the interannual variation in rates of mortality due to cannibalism are sufficient to cause major recruitment variations. One would suspect that variability in egg mortality rate could arise from the 70% of egg mortality not due to cannibalism. Off California, Theilacker (1988) has estimated that the rate of northern anchovy egg consumption by juvenile and adult euphausiids may account for 28% of the egg mortality. Other influences on recruitment could arise from copepod predation on yolk-sac larvae (Lillellund and Lasker 1971) and predation of Pacific mackerel on juveniles (Methot 1986[6]).

To manage variable stocks like the sardine and anchovy it may be sufficient to monitor the age structure of the catch and the production and survival of the embryonic stage (Methot and Lo 1987[7]). A decrease in the number of older, highly fecund, spawning age classes will decrease effective population fecundity. In filter feeders like sardine and anchovy, cannibalism by younger age classes may lower the survival of eggs. Thus, merely by monitoring age structure and egg survival one can project when large, unusually successful year classes are possible. New techniques for monitoring juvenile abundance and growth will be required when a sardine or anchovy fishery becomes so intensive that an early recruitment prediction is necessary.

ACKNOWLEDGMENTS

The late Dr. Reuben Lasker was the mentor and enthusiast for work on population assessment and for survival research on the schooling coastal pelagic fishes around the world, particularly sardine and anchovy. We want this manuscript to be part of the celebration of Lasker's career. We thank Romulo Jordan S., Julio Valdivia G., and Isabel Tsukayama, science directors of the Instituto del Mar del Peru during this research, and their research staff. We also acknowledge the support of Wolf Arntz in providing the travel and subsistence of the senior author during this series of studies off Peru. We also prize the assistance of four graduate students from Peru: Veronica Blaskovich, Wilmer Carbajal, Emperatriz Luyo, and Jorge Oliva. We appreciate the assistance of Izadore Barrett, John Butler, John Hunter, Alec MacCall, and Daniel Pauly in reading this manuscipt. We thank the Captain and crew of the IMARPE's research trawler, *Humboldt*.

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Ageing and Back-Calculating Growth Rates of Pacific Herring, *Clupea pallasii*, Larvae by Reading Daily Otolith Increments

Erlend Moksness and Vidar Wespestad

ABSTRACT: Newly hatched Pacific herring, *Clupea pallasii*, from eastern Bering Sea were released into an outdoor concrete basin and raised on natural plankton. The larvae were sampled frequently during the first two months, and a growth curve for that period was established. Otoliths from 52 herring larvae, collected over the entire experimental period, were examined for daily increments. Increments were formed on a daily basis from the end of the yolk-sac stage (age 8 days) and were found to be independent of the growth rate of the herring larvae. The increment widths, however, reflected the growth rate of the larvae.

Otoliths have been used to estimate daily age and growth since Pannella (1971) reported that the number of primary increments in otoliths approximated daily deposition. Brothers et al. (1976) raised northern anchovy, *Engraulis mordax*, and California grunion, *Leuresthes tenuis*, from eggs in the laboratory and verified that increment formation occurred daily. Jones (1986) found that daily increment analysis had been applied to at least 29 species of larval fish to estimate age, but validation of the technique was based on laboratory observations that may be invalid for wild populations. Atlantic herring, *Clupea harengus*, have been investigated for daily increment formation (Gjøsaeter and Øiestad 1981; Geffen 1982; Lough et al. 1982; Jones 1985; Messieh et al. 1987). Contradictory findings by various authors have created controversy concerning whether Atlantic herring deposit growth increments on a daily basis. Gjøsaeter and Øiestad (1981) found 99 increments in 97 d herring grown in a large outdoor enclosure; however, their sample size was too small to be conclusive (Jones 1986).

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The early life history of Pacific herring, *Clupea pallasii*, from the eastern Bering Sea was studied in the same enclosure as Gjøsaeter and Øiestad's (1981). All the herring were spawned on the same day, and larvae hatched over a 3 d period. Otoliths were examined periodically during the experiment and from surviving individuals at the termination of the experiment.

MATERIAL AND METHODS

Pacific herring eggs were collected from the spawning grounds in Bristol Bay, AK at low tide on 24 May 1986. The eggs collected had been deposited between 22 May and 23 May on intertidal rockweed, *Fucus* sp. Water temperature at the time of spawning was 4.5°C and salinity was 30‰. Further spawning did not occur (before or after) in the area in which the eggs were collected. *Fucus* fronds with light egg coverage (1–2 egg layers) were collected at random within the spawning area, packed into half liter plastic bags, filled with seawater, and sealed. A total of 25 bags were filled with about 2,000 eggs/bag. The bags were placed in insulated shipping containers with gel ice, which were shipped via air to the Flødevigen Biological Station in Arendal, Norway. Upon arrival at Flødevigen the eggs were unpacked and placed in hatching boxes, which were supplied with flowing seawater at 7.7°C and at salinity of 32‰.

The eggs began hatching on 10 June 1986 and finished by 12 June 1986. Fifty percent hatching (11 June) was defined as day 0 (age = 0) in the experiment. Newly hatched larvae were collected from incubation boxes in white plastic cups in groups of 5–25, counted, and transferred to 5 L cylinders, which were placed in an 8.1°C water bath. A total of 25,200 larvae hatched from an estimated total of 50,000. The eggs were not treated during incubation and a heavy fungus growth developed. This caused most of the egg mortality.

On 13 June (age 2 days) 24,840 larvae were released into a large artificial outdoor basin—2,000 m^3 in volume, 600 m^2 in surface area, and 3.5 m at maximum depth. The basin had been filled with seawater pumped from a depth of 19 m. At the time the larvae were introduced, phytoplankton and zooplankton production was high. The basin was drained on 12 August, and the remaining herring larvae in the basin were collected (age = 62 days).

The larvae in the basin were sampled daily using a two-chambered plankton net of 500 μm mesh and a total sampling area of 0.3 m^2. The net was drawn diagonally across the basin at a depth of 2 m and the total volume sampled was 7.5 m^3. All the sampled larvae were preserved in 80% buffered ethanol. A more detailed description of the basin experiment is given in Wespestad and Moksness (1989)[1]. The standard length (snout to the tip of the notochord or hyplural plate) of the larvae/juveniles were measured to the nearest 1.0 mm. The largest otoliths, the sagittae, were removed and mounted on a glass plate with clear nail polish. The dry weight of each individual was measured to the nearest ±1 μg, after drying at 60°C for 24 hours. Otoliths of herring juveniles over 30 mm had to be ground, to expose growth rings. This was done with fine grit paper (30 μm and then 0.3 μm). The maximum magnification that could be used to read the growth rings in the microscope was × 400, owing to insufficient light penetrating the section. Table 1 gives an overview of the number of larvae used in otolith analyses. A detailed description of the otolith analyzing system and the method used are given in Andersen and Moksness (1988).

TABLE 1.—The number of larvae examined for daily increments by date.

Date	Age	Number examined
25 June	14	1
3 July	22	2
10 July	29	5
14 July	33	5
18 July	37	5
21 July	40	5
27 July	46	10
12 Aug.	62	19

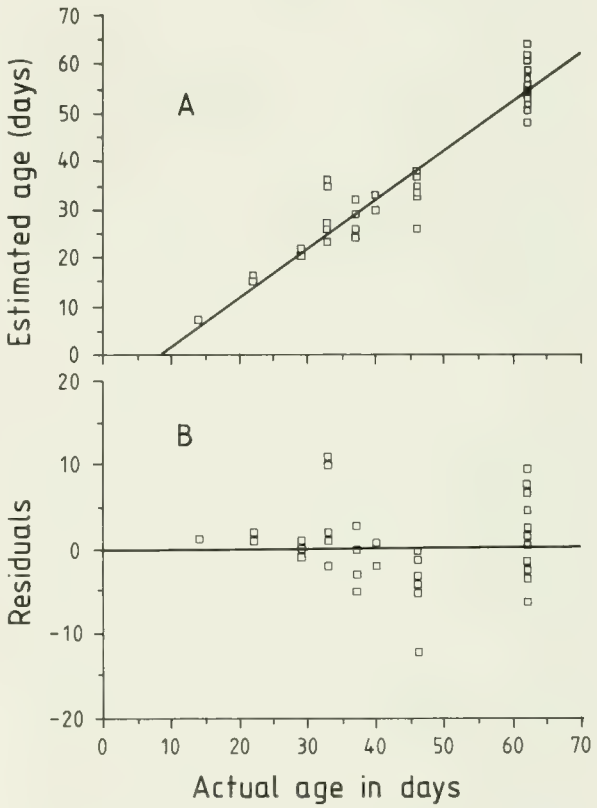

FIGURE 1.—Relationship between estimated and actual age of Pacific herring in days (A), $y = -8.3 + 1.0144\,x$, $r = 0.96$; and the pattern of the residuals (B).

RESULTS

The relationship between the estimated age (estimated number of rings) and the actual age of the herring larvae is shown in Figure 1. The residuals are shown in the same figure. The relationship was linear, and the deposition rate was not significantly different from one increment per day from age 8 days of the larvae (t-test; t = 0.08, df = 50). The residuals were equally distributed around zero indicating no trend in the data. The discrepancy did not tend to change sign or range with the age of the larvae (Fig. 2), indicating that the frequency of daily increments in the otoliths did not change with the age of the larvae. The standard deviation of estimated age from real age was ±4.2 days with a range from −12 to +11 days; therefore, there is little correlation between estimated age and length (Fig. 3). Apparently, there is no relationship between the rate of otolith ring deposition and larval growth.

All three relationships between larval standard length and otolith radius exhibited a good fit to the data (Fig. 4, $r > 0.96$), but the first, the

[1]Wespestad, V., and E. Moksness. 1989. Observations on the growth and survival during the early life history of Pacific herring, *Clupea pallasi*, from Bristol Bay, Alaska, in a marine mesocosm. Submitted Fish. Bull., U.S.

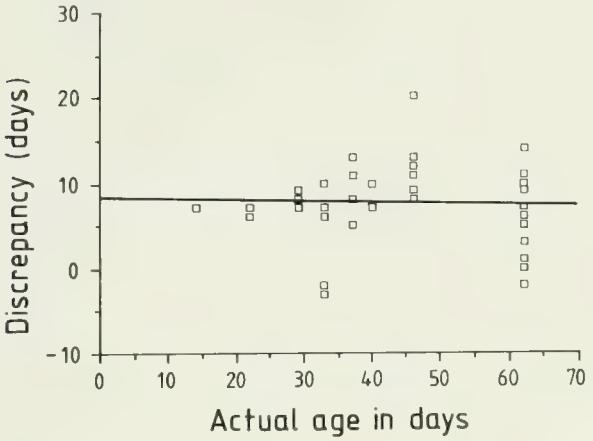

FIGURE 2.—Discrepancy between estimated age (real age minus estimated age) and actual age of Pacific herring as a function of actual age. $y = 8.3 - 0.014\,x$, $r = 0.05$.

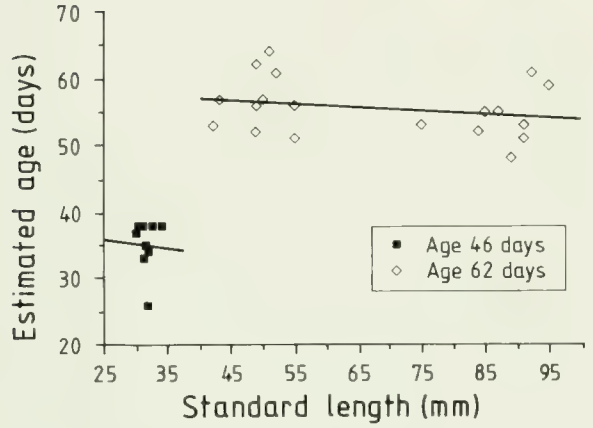

FIGURE 3.—Relationship between estimated age and standard length in Pacific herring larvae of same age. Age 46 days: $y = 39.63 - 0.14\,x$, $r = 0.04$; age 62 days: $y = 59.53 - 0.06\,x$, $r = 0.27$.

fourth order polynomial, provided the best fit to the initial length of the larvae.

The average daily growth rate (±1 SD) calculated from all otoliths with the fourth order polynomial is presented in Figure 5 along with the estimated minimum, maximum, and average growth rate obtained from the herring measured at termination of the experiment. The relationship shows that there is a high similarity in the trends of the growth curves between the different age groups. The daily growth rate calculated from the standard length of the larvae at termination of the experiment showed an average of 0.66 mm/d, a minimum of 0.31 mm/d, and a maximum of 1.48 mm/d. Estimation of the average growth rate, using these data, gives an average growth rate of 0.73 mm/d.

DISCUSSION

The results of this study show evidence of daily increments in the otoliths of Pacific herring, agreeing with earlier investigations on the same species (McGurk 1984a). A difference of eight days was observed between the estimated

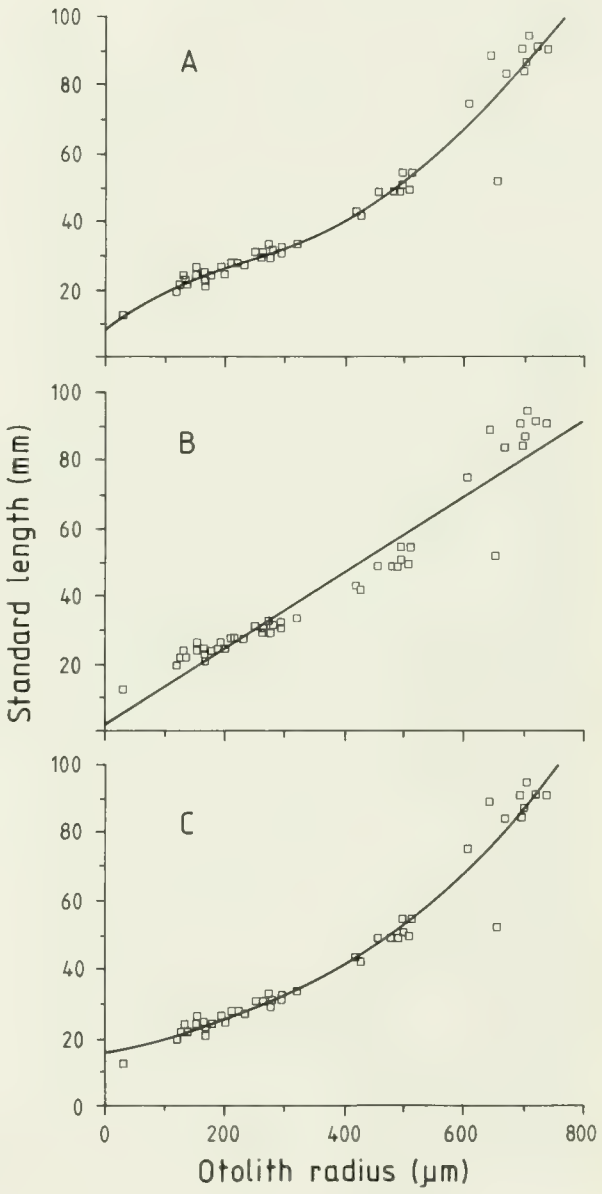

FIGURE 4.—Relationship between otolith radius (x) and standard length (y) of the Pacific herring larvae. A: $y = 8.1461 + 0.1542\,x - 4.875 * 10^{-4}\,x^2 + 9.651 * 10^{-7}\,x^3 - 5.038 * 10^{-10}\,x^4$, $r = 0.98$. B: $y = 2.6738 + 0.1123\,x$, $r = 0.96$. C: $y = 15.6952 * 10^{(0.0011\,x)}$, $r = 0.98$.

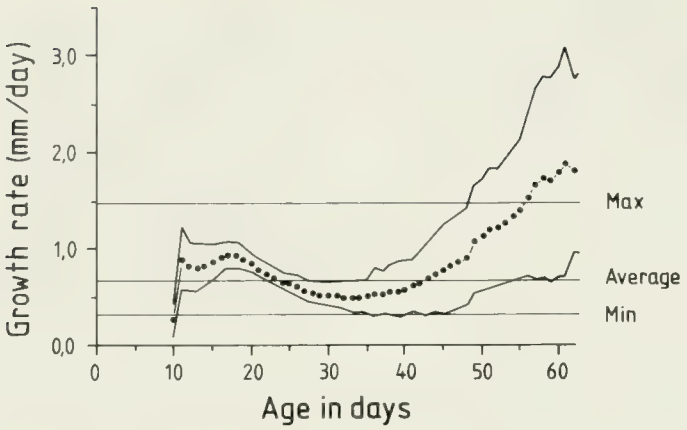

FIGURE 5.—The average daily growth rate (mm/day) estimated from otolith analyses (·) with ±1 SD. The minimum (min), average, and maximum (max) growth rate (mm/day) calculated from Pacific herring surviving to the termination of the experiment (day 62) are indicated.

and the actual age of the larvae; this difference corresponds well with the end of yolk-sac stage of the same larvae (Wespestad and Moksness fn. 1); it is three days later than that found by McGurk (1984b) for Pacific herring larvae at the same temperature (8.0°C).

The results are the same as earlier investigations on Norwegian spring spawning herring in a 4,400 m^3 outdoor basin (Gjøsaeter and Øiestad 1981) in which herring form one otolith increment per day. However, the results of one increment per day contradicts findings from laboratory experiments in which otolith increments were not formed daily. Geffen (1982) on Atlantic herring and McGurk (1984a) on Pacific herring found the growth rate of the larvae and the number of increments in the otoliths to be correlated, while our results show a poor correlation between growth and daily increments. The expected standard deviation was ±1 day, based on the observed range in hatching time; however, the estimated variation was much greater than this. A possible explanation for this discrepancy might be that the minimum growth rate (0.31 mm/d) observed in this study was greater than growth rates observed in laboratory studies.

Geffen (1982) reported that growth coefficient tended to increase with the increase in size of aquarium used—from the 120 L laboratory tanks up to 4,000 m^3 mesocosms. The difference in data between experiments using small and experiments using large rearing tanks results from an inability of larvae to form daily increments at low growth rates (Moksness et al. 1987). In our work, the average growth rate corresponded to the growth rate observed in nature. Checkley (1982)[2] reported otolith increments and fish length for juvenile herring captured in Bristol Bay in autumn 1981. From these data, we estimated the average daily growth rate over the first summer of life to be 0.74 mm/d, which is similar to the average growth rate observed in this experiment. Therefore, it appears that conditions in the basin were similar to the average conditions larvae experience in its natural habitat.

Otolith increment size was well correlated with the measured growth in standard length of the larvae. The preferred growth model (see Figure 4a), gave a good fit to the observed values, however small the sample size and especially for the smallest larvae, but the growth model did not rule out the applicability of other models. An exponential model might fit better with more available data. When fitting the data on dry weight of the larvae to the radius of the otolith, a very good fit was observed for the exponential equation.

The resulting daily length increment from the fourth order polynomial growth model approximated the calculated daily length increment based on observed length-at-age reported by Wespestad and Moksness (fn. 1). By estimating the relationship between the standard length of the larvae and the radius of the otolith, the daily length-increment of the fish could be described.

[2]Checkley, D. M. 1982. The ageing of juvenile Pacific herring by otolith analysis. Final Report, NOAA contract 82-ABA-1001. Northwest and Alaska Fisheries Center.

The range in the residuals and deviations reported in this paper are believed to be, in part, due to the use of × 400 magnification. This has been shown to be too low to give good resolution of the otoliths (Campana et al. 1987).

Three general conclusions can be drawn from this study: 1) Daily otolith increments in Pacific herring larvae are true daily increments at normal rates of growth. 2) The results, showing poor correlation between length and age, suggest that age in days can be estimated only from direct ageing and that attempts to establish age from age-length relationships may produce significant errors. These types of error may be important in stock separation studies such as distinguishing between spring and autumn spawned herring (Fossum and Moksness 1988). 3) Mesocosms may be a more appropriate environment for studying marine fish larvae and juveniles than laboratory-sized rearing tanks. Growth appears to be influenced by container size. Mesocosms have been shown to produce growth rates for other species such as capelin, *Mallotus villosus*, similar to that observed in the field (Gjøsaeter and Monstad 1985).

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Egg Size, Female Effects, and the Correlations Between Early Life History Traits of Capelin, *Mallotus villosus*: An Appraisal at the Individual Level[1]

R. Christopher Chambers, William C. Leggett, and Joseph A. Brown

ABSTRACT: The authors examined the within-individual correlations between egg quality (quantified by yolk volume) and early life history traits in capelin, *Mallotus villosus*. The commonly reported generalization—large eggs produce large larvae that subsist longer on endogenous energy reserves—was not supported by our analysis. Post-hatching lifespan of unfed larvae did not vary with initial egg yolk volume, yolk-sac volume at hatching, or size at hatching. The only correlate of post-hatching lifespan was a direct relationship with oil globule volume at hatching. Size and age at hatching covaried directly, but hatching later exacted a cost on yolk reserves. Significant female influences on these early life history traits of offspring were found. Initial egg yolk volume and oil globule volume at hatching contributed most to the rejection of the null hypothesis of no female effect. None of the early life history traits examined was correlated with female size, but female condition and lipid indices were directly correlated with average initial yolk volume.

Most individuals in marine fish populations die before feeding begins (Hewitt et al. 1985; Ware and Lambert 1985; McGurk 1986; Taggart and Leggett 1987a). Central to much of Reubin Lasker's work was the role of timing in survival during these early life stages. This was explicit in his early papers on temperature-dependent developmental rates (Lasker 1962, 1964; Zweifel and Lasker 1976) and became an implicit part of his "stable oceans hypothesis" (Lasker 1975, 1981, 1985), which postulates that coincidence in the timing of physical oceanographic conditions favoring food production and the timing of first feeding in fish larvae is critical to larval survival. Peterman and Bradford (1987) recently evaluated interannual variability in both the frequency of turbulence-generating winds and the survival of northern anchovy, *Engraulis mordax*, larvae and found an inverse relationship between these two events.

Temporal matching of resources and consumers is one of degree as timing of early life history (ELH) events varies even under constant conditions (Chambers and Leggett 1987, 1989; Chambers et al. 1988). Knowledge of the within-population variation in ELH traits is, therefore, crucial for estimating the number of larvae that establish feeding, and thus retain the potential for recruitment to the fishery. To Lasker's credit, his temperature-dependent development experiments in sardines, *Sardinops sagax*, were conducted on individual embryos isolated in incubation chambers in order "to assess their individual variability of development and growth" (Lasker 1964, p. 399). While variability in hatching age within and across temperatures is apparent from Lasker's plot of age at hatching of individual sardines versus temperature, the potential relevance of this variability to survival was not discussed further.

Variable provisioning of energy reserves to embryos is one of several mechanisms that could generate variability in size at hatching, in size and age at first feeding, in ability to withstand starvation, and, consequently, in survival to and during the critical switch from endogenous to exogenous nutrition. It is often reported that larger eggs produce larger larvae that subsist longer without food (e.g., Blaxter and Hempel 1963). Although this has become doctrine in reviews of marine fish early life histories (Blaxter 1969, 1988; Hempel 1979; Hunter 1981; Rothschild 1986), at least one of three caveats applies to work that has led to this generalization. 1) Eggs were grouped either by size (e.g., small vs.

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large) or source (e.g., full-sibling groups) and the analysis of the influence of egg size on ELH traits was conducted among these groups. Correlations, when reported, were based on the average trait values in these groups. Such analyses obscure variation in and correlation between traits at the individual level—where natural selection acts. 2) Simple correlations were calculated. These may reflect the response of two traits to a third covarying trait rather than appraise the influence implied. 3) Egg size was confounded with other factors not explicitly considered (e.g., different source populations, seasons of spawning, years, and ages of females). The influence attributed to egg size is, therefore, equivocal. These are important limitations. The estimates of relationships between egg size and subsequent ELH traits so derived cannot be presumed to be of the same magnitude or statistical significance as those from within-individual observations. The conclusions of previous studies must be viewed as provisional demonstrations of associations of egg size with the ELH traits considered.

The extent to which relationships exist at the individual level between egg size, hatchling size, and prestarvation lifespan remains unanswered. In this paper we analyze such ELH trait covariation in capelin, *Mallotus villosus*. We address two questions: First, which pairs of ELH traits covary when evaluated at the individual level while (statistically) holding other traits constant? Of particular interest is which, if any, of these traits vary with egg quality. Second, is the pattern of ELH trait variation attributable to maternal influences?

METHODS

Spawning capelin were collected on 23 and 25 June 1988 at spawning sites in eastern Newfoundland, Canada (lat. 49°39′N, long. 52°41′W). These capelin were held in a 1,000 L flow-through tank at the Marine Science Research Laboratory, Logy Bay, Nfld. until 28 June when crosses were performed. Eggs from each of 10 females were fertilized with milt from one male. This provided a range of eggs sizes and created the potential for female effects on ELH traits of offspring while minimizing male influence.

Yolk diameters of 12–15 eggs per female were measured at 20–28 h postfertilization at a magnification of 40×. These embryos were in the blastula stage and their yolks remained approximately spherical. Embryos were then transferred individually to separate wells of 12-well tissue culture plates. These plates served to limit possible interaction among incubating embryos (e.g., bacterial growth on dead eggs) by keeping embryos at least 3.5 cm apart. In total, 142 eggs were housed in 12 plates, each containing 1 or 2 fertilized eggs per female. Each set of 4 plates was submerged to a depth of 10 cm in a separate plastic tank containing static seawater; thus, all embryos in a tank were exposed to the same seawater. This seawater was filtered to 1 μm, sterilized with ultraviolet light, and changed every 2 days to ensure sufficient levels of oxygen for the developing embryos. All three static seawater tanks were placed in a common water table maintained at 9.5 ± 0.49°C (mean ± SD). At the late eyed stage, embryos were transferred individually to separate 125 mL glass jars containing 100 mL of filtered, sterilized seawater. Embryos in jars occupied the same location in the water table as they had before transfer. Fluorescent lamps in the laboratory were set to 18 h light, 6 h dark.

Embryos were inspected daily and their day of hatching recorded. Hatchlings were anaesthetized (MS-222, 25 mg/L), measured, revived, and returned to their jars. Total length (TL), length and height of yolk, and diameter of oil globule were measured. Larvae were inspected daily until their death, which was inferred if a larva did not respond to gentle tapping of its holding jar. Deformed hatchlings (3.5%) and those failing to escape the egg membrane (1.4%) were excluded from analyses.

Immediately after spawning, each female was measured (standard length, SL) and frozen. Subsequently, but within 2 months, females were thawed and somatic weights determined. Constant dry weights were achieved after oven drying at 60°C for 48 hours. These dried carcasses were ground and their lipids were extracted by flooding with diethyl ether and decanting (Dobush et al. 1985). Constant lean, dry weights were obtained after three cycles of lipid extraction. Indices of somatic condition (wet weight/SL) and lipid condition (extractable lipid weight/lean dry weight) were calculated for each female.

We analyzed six ELH traits: initial yolk volume (Y1), total length at hatching (TL), yolk volume at hatching (Y2), oil globule volume at hatching (G), age at hatching (H), and posthatching lifespan (L). Initial egg yolk and oil globule at hatching were approximately spherical and we estimated their volumes from their diameters.

Yolk at hatching was approximately a prolate spheroid and we estimated this volume from measurements of length and height of the yolk complement minus the volume of the oil globule it contained.

We used initial yolk volume rather than initial egg volume to quantify egg quality because it better represents the energy content of the egg. We chose posthatching lifespan over the more frequently used time to yolk-sac depletion or time to irreversible starvation ("point-of-no-return", Blaxter and Hempel (1963)), because the latter are much more difficult to determine accurately. We assumed a high correlation between these components of posthatching lifespan for unfed larvae. In support of this assumption we calculated a correlation of $r = 0.88$ ($P < 0.001$) between the interval from hatching to yolk-sac depletion and the interval from yolk-sac depletion to irreversible starvation, using data from 25 marine fish species presented by McGurk (1984).

We accounted for the potential influence of environmental (laboratory) variation on ELH measurements by using location of the embryos and larvae in the water table as a blocking variable. In addition, jars were inspected for hatchlings, and hatchlings were measured, in sequence by block. Block specification thus represented chance differences among the three static tanks; locational differences (which might include effects of slight temperature or light gradients on any of the ELH traits); and effects of unavoidable delays in measuring hatchlings. These delays were caused by the time required to measure the hatchlings. As an extreme example, 30 hours were required to measure all larvae hatching on the modal hatching day.

We employed a two-way randomized block experimental design with female parent as the treatment of interest (i.e., are there significant differences among females in the ELH traits of their offspring?). This design allowed us to determine both the female effect on ELH traits and the within-individual correlations between those traits. The design was unbalanced because the number of eggs used varied (12–15 per female) and some mortality occurred before hatching.

We treated the six traits as a multivariate response and analyzed these as a random-effects multivariate analysis of variance (MANOVA) with the general linear model

$$(\mathrm{Y1, TL, Y2, G, H, L}) = \mu + \mathrm{female} + \mathrm{block} + \mathrm{female} \times \mathrm{block} + \epsilon.$$

The six ELH traits of the response vector are defined above, μ is the overall mean, *female* codes for females 1–10, *block* codes for tank/location/monitoring order 1–3, and ϵ is random error from the model.

We calculated partial correlations between all pairs of traits from residuals remaining after the effects of block and the remaining four traits (considered for this procedure as covariables) had been statistically removed. We also calculated simple correlations between all pairs of traits based on average group values (common female parent), as has been the practice in previous work. These correlations were compared with the partial correlations to assess differences in estimated correlations based on the two approaches.

We evaluated the female effect on the trait vector with Wilk's lambda criterion (Timm 1975). After rejecting the null hypothesis of no female effect we gauged the contribution of each trait to this result. This was done by examining the magnitude and sign of the correlation between each trait mean and the standardized and adjusted discriminant function that maximized among-female differences (Timm 1975; Wilkinson 1975). We also compared the MANOVA findings with standard F-tests and with percentage of the total variance due to female source as calculated from univariate ANOVA's on each ELH trait. We assessed the influence of female condition on the ELH traits of her offspring by estimating the simple correlation between each family-average ELH trait and female size, condition index, and lipid index.

Prior to analysis we log transformed initial yolk volumes and yolk and oil globule volumes at hatching. MANOVA, discriminant analysis, and partial correlations were performed on SYSTAT (Wilkinson 1988) and the variance components were estimated using SAS (SAS Institute, Inc. 1987).

RESULTS

Survival to hatch was over 98%. The quantity of variation in initial yolk volume, age at hatching, and age at death (C.V. (= SD/mean) = 0.15, 0.03, and 0.24, respectively) was comparable to values reported for other species (cf. Chambers et al. 1988). Length, yolk, and oil globule volume at hatching were more variable than expected (C.V. = 0.08, 0.98, and 1.44) owing partly to their rapid change during the 1–2 days after hatching when measurements were taken. By

measuring larvae in block sequence we reduced this variance due to ontogeny in our analyses of correlations and female effects.

Correlations Between ELH Traits

There were seven significant partial correlations between the ELH traits (Fig. 1). These correlations measure whether or not a change in one trait is associated with a change in the other while holding the remaining (four) traits constant. Size, yolk reserves, and age at hatching all covaried directly with initial yolk volume. Hatchling size increased with age at hatching, but yolk reserves at hatching were negatively related to age at hatching. Yolk and oil globule volume at hatching covaried directly. Oil globule volume at hatching was the only trait that covaried with posthatching lifespan; all else equal, larvae with larger oil globules lived longer.

It is important to note the trait pairs that failed to show associations. Oil globule volume at hatching did not vary with initial yolk volume. Length at hatching was independent of yolk or oil globule volume at hatching. Futhermore, posthatching lifespan was not related to initial yolk volume, length, age, nor yolk volume at hatching.

The correlations between ELH traits based on family averages differed from the partial correlations calculated within individuals (Table 1). The sample size of family groups was small (n = 10), hence, caution is required when assessing the pattern that emerged. First, there were no neg-

TABLE 1.—Simple correlations between early life history traits of capelin, *Mallotus villosus*, calculated from family averages (df = 8). *P<0.05, **P<0.01.

Trait	(1)	(2)	(3)	(4)	(5)	(6)
1) Egg yolk volume	1.00	0.55	0.53	0.36	0.43	0.59
2) Length at hatching		1.00	0.58	0.45	0.32	0.42
3) Yolk volume at hatching			1.00	0.80**	0.08	0.54
4) Oil volume at hatching				1.00	0.13	0.68*
5) Age at hatching					1.00	0.57
6) Posthatching lifespan						1.00

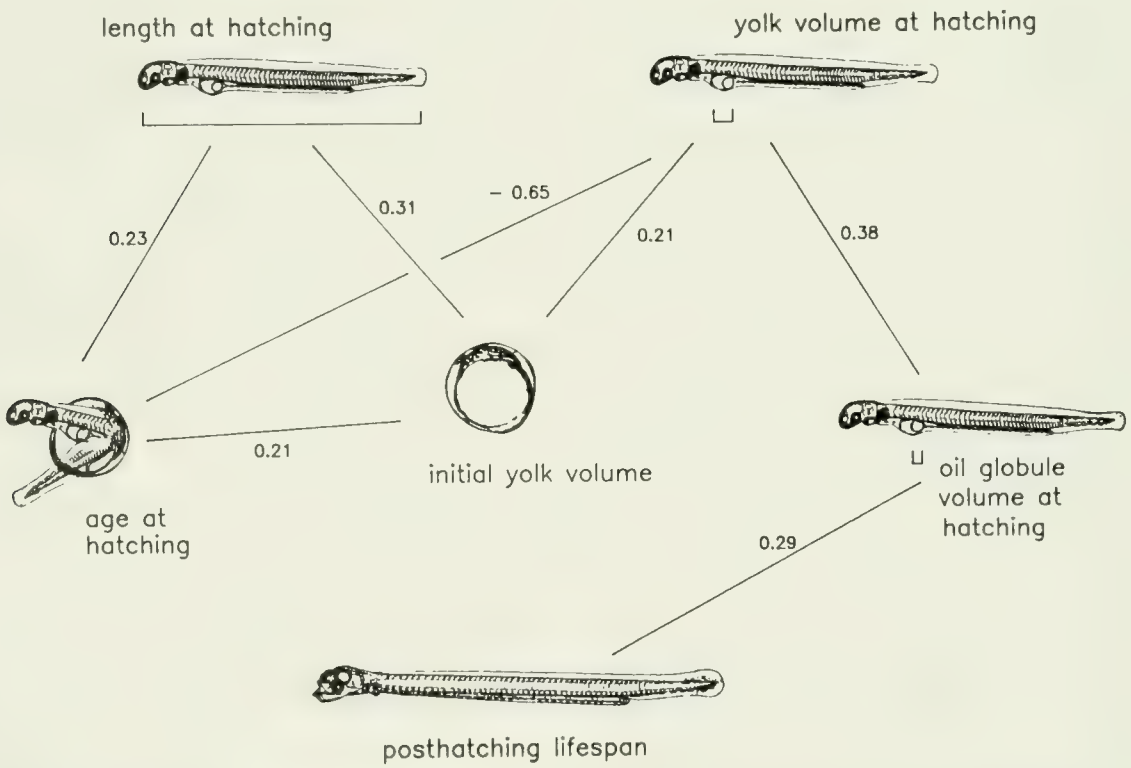

FIGURE 1.—Early life history traits of capelin, *Mallotus villosus*, subjected to analyses and the within-individual partial correlations between traits. Only significant correlations are shown ($P < 0.05$, df = 126).

ative correlations between traits. Second, while the correlation between yolk volume and oil globule volume at hatching and between oil globule volume and posthatching lifespan remained significant ($P < 0.05$), the magnitude of the correlations between posthatching lifespan and all other ELH traits approached significance. This pattern of correlations derived from family averages suggests that offspring from eggs with large yolk volumes are larger at hatching, hatch later, have larger yolk reserves and oil globules at hatching, and live longer than do offspring of females producing eggs with less yolk. This pattern is consistent with results of most previous reports based on average trait values.

Female Effects on ELH Traits

Initial egg yolk volume varied among females (Fig. 2). Female identity significantly influenced the set of six ELH traits (Wilk's $\lambda = 0.0001$, $F = 6.1$, df = 54, 70, $P < 0.0001$). Initial yolk volume and oil globule volume at hatching were the predominant traits contributing to among-female differences (Table 2). Univariate ANOVAs supported the MANOVA result; all traits varied significantly among females and the percentage of variance due to female was greatest for initial yolk and oil globule volume at hatching (Table 2). None of the family-averaged ELH traits was significantly correlated with female size. However, the average initial yolk volume of the egg was directly related to condition and lipid indices of the female (Table 2).

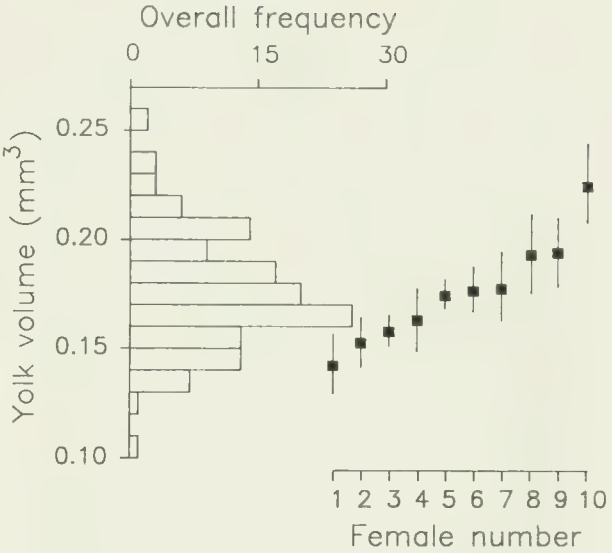

FIGURE 2.—Overall frequency distribution of initial egg yolk volumes and partitioned variation (means ± 2 SD) of yolk volumes by female for capelin, *Mallotus villosus*. A total of 142 eggs were measured from 10 females. Females are ranked by average yolk volumes of their eggs.

DISCUSSION

Correlations Between ELH Traits

Our observations of positive within-individual relationships between initial yolk volume and

TABLE 2.—Contributions of early life history traits (ELH) of capelin, *Mallotus villosus*, to the rejection of the null hypothesis of no female effect, and correlations between these traits and properties of female parents used. (1) Correlations between ELH trait means and the standardized discriminant function that maximized among female differences. (2) Percentage of total variance in each ELH trait due to female effect. Correlation between ELH trait means and female size (3), female condition index (4), and female lipid index (5). The magnitude of the correlation between ELH traits and the discriminant function reflects the contribution of a trait to rejection of the multivariate null hypothesis of no female effect. The eigenvalue associated with this discriminant function accounted for >77% of the variation among the ELH traits. * $P < 0.05$, ** $P < 0.01$.

	Egg yole volume	Length at hatching	Yolk volume hatching	Oil volume hatching	Age at hatching	Posthatch lifespan
1) Discriminant function	0.43	0.15	0.11	0.35	0.10	0.21
2) % variance	71.30	17.21	2.91	66.67	12.01	24.39
3) Female size						
SL	0.36	0.00	0.35	0.30	−0.41	−0.05
Wet somatic weight	0.61	0.18	0.53	0.43	−0.22	0.24
4) Female condition	0.65*	0.22	0.57	0.46	−0.17	0.29
5) Female lipid	0.85**	0.44	0.43	0.31	0.34	0.55

hatchling length, and between initial yolk volume and yolk volume at hatching agree with most previous reports based on grouped data (reviewed in Blaxter 1988). The positive relationship between initial yolk volume and age at hatching differs from the generally reported pattern of no association. Moreover, the increase in length with age at hatching we observed is contrary to that reported by Bengtson et al. (1987) who analyzed daily hatching cohorts within families. Hatching late, however, appears to occur at the expense of yolk reserves (Fig. 1). This negative relationship was not present in the correlations based on family averages (Table 1).

Neither initial yolk volume, length at hatching, nor yolk volume at hatching was related to posthatching lifespan when evaluated within individuals. This contrasts both with our correlations based on family averages and with previous generalizations (from group averages) that large initial egg size leads to hatchlings that survive longer in the absence of food (Blaxter 1988). The only association with posthatching lifespan that we detected was the direct influence of oil globule volume at hatching. Our data indicate that if all else were held constant, an increase in oil globule volume delays the time to starvation of individual larvae. This prolonged posthatching lifespan should increase the chances of encountering suitable food before irreversible starvation and, thus, the chances of survival. Lipids, whether aggregated in oil globules or dispersed throughout the yolk, appear to serve primarily as energy reserves (Blaxter 1969). Conservation of oil globules (relative to yolk) has been reported for species that have oil globules in their yolk sacs (e.g., May 1971; Bagarinao 1986) although oil globules may also serve to regulate buoyancy.

A variety of evidence argues for advantages of large size at hatching (a positive correlate of initial yolk volume). Larger larvae have greater mouth widths (Shirota 1970), have greater success in establishing feeding (Knutsen and Tilseth 1985), are more effective predators (Blaxter and Staines 1970; Hunter 1981), consume a greater range of prey sizes (Hunter 1981), and have higher survival when predators are absent (Rosenberg and Haugen 1982; Henrich 1988) or present (Lilleland Lasker 1971; Bailey 1984; Folkvord and Hunter 1986; Purcell et al. 1987). Although many of these studies compared larvae of two or more groups that differed in age as well as size, the results are likely to apply to the finer size differences among contemporaries. Mortality has also been reported to be size specific and to be concentrated early in the life cycle in natural populations (Crecco et al. 1983; Smith 1985; Rice et al. 1987; Savoy and Crecco 1988).

The cost of producing large eggs is frequently evaluated under the assumption of a trade-off between egg size and egg number (Svardson 1949; Smith and Fretwell 1974). This assumption has led to optimality derivations for balances between size and number of eggs under given conditions. Observed patterns of size and number of eggs among species, populations, or reproductive modes are then evaluated in light of the predicted optima (Ware 1975; Sargent et al. 1987; Tanasichuk and Ware (1987)). The correlations between ELH traits we observed suggest that egg size expresses reciprocity with other ELH traits to which optimality methods may be applied. For example, a corollary of the direct relationship between length and age at hatching in capelin is that an inverse relationship exists between length at and developmental rate to hatching (the reciprocal of age at hatching). If daily mortality rates are greater in the embryonic than in the larval period, an extended embryonic period is seen as a cost of being large at hatching.

This optimality approach is inherently deterministic. It does not explicitly admit within-population and within-female variation in egg size (Fig. 2) and in other ELH traits we observed. Rather, this variation is viewed as failure to achieve the optimal trait value or combination of trait values. In contrast, we consider trait variation itself to be adaptive. For capelin, the emergence of larvae from their intertidal incubation sites into the nearshore water is linked to the episodic occurrence of relatively warm water and nearshore turbulence, generated by onshore winds and coastal water mass exchanges (Frank and Leggett 1981a, 1983; Taggart and Leggett 1987b). The attainment of a developmental stage from which an embryo can be induced to hatch (e.g., through a sudden rise in temperature and/or turbulence) or its nutritional state at the time of emergence, if previously hatched (Frank and Leggett 1982), are important determinants of survival during early pelagic life. However, the intertidal incubation zone is variable for capelin in three fundamental ways. First, temperature directly influences developmental rates of embryos. Local temperatures in the intertidal substrate oscillate up to 10°C (Frank and Leggett 1981b) with tidal cycle. Thus, there are large microsite differences in

temperatures and developmental rates. Second, the small particle substrate to which eggs adhere is motile, mixing in all three dimensions with wave action. Third, onshore winds promote hatching and/or release of larvae from these beaches, yet their frequency is highly variable within and between years (Frank and Leggett 1981a, 1983; Leggett et al. 1984; Taggart and Leggett 1987b). From the maternal perspective, the time of the transition of her offspring from beach residence to the pelagic mode is unpredictable owing to these three sources of variation. It appears unlikely that a single optimal solution exists for developmental rate, size at hatching, or energy reserves. Additional examples of intrapopulation and intraclutch variation in early life history traits, and of theoretical bases for the maintenance of this variation in unpredictable environments, is provided in Capinera (1979) and Kaplan and Cooper (1984).

Female Effects on ELH Traits

Variation in egg quality is a sum of genetic and environmental factors. We have no evidence that egg size is heritable in capelin. We did not detect a male effect or heritable variation in size at hatching in another study involving 11 male capelin each mated with 3 females (Chambers and Leggett unpubl. data), yet there, as here, significant differences among females were evident in both initial egg and hatchling sizes. Our determination of a direct relationship between condition and lipid indices of females, and initial egg yolk volume probably reflects a predominant environmental component to the observed variation in egg quality (yolk volume) and its correlates. The degree of influence from environmental sources of maternal effects on ELH traits probably depends largely on conditions experienced by a female during the time that energy is being acquired and converted towards oogenesis, particularly her feeding rate (Hislop et al. 1978) and encountered temperatures (Tanasichuk and Ware 1987). If so, these largely nongenetic maternal effects have the potential to modulate the expression of critical ELH traits and modify the survival pattern that would otherwise be exhibited if the initial provisioning of yolk reserves were at par throughout the population. Well-endowed individuals could thus be buffered against selection in the yolk-dependent period with, perhaps, residual effects later in larval life. The inverse correlation between size of mother and age at smoltification of her progeny in sockeye salmon, *Oncorhynchus nerka*, as reported by Bradford and Peterman (1987) may be such a residual effect.

Covariation Within Individuals and Variation Within Groups

Relationships we observed between ELH traits clearly show that simple correlations based on group data may support, but may also be inconsistent with inferences drawn from analyses at the individual level. Only estimates of variation and correlations between traits that are based on individual-level observations are grounded on the same scale that natural selection primarily acts (Sober 1984). Caution must be exercised when extrapolating from group differences or correlations based on averages to influences of one trait on another, to potential advantages conferred on individuals, to dynamics of populations, or to evolution of life histories.

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A Laboratory Study of the Bioenergetics of Larval Walleye Pollock, *Theragra chalcogramma*

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ABSTRACT: Rates of growth, oxygen consumption, and ingestion were measured for larval walleye pollock, *Theragra chalcogramma*, in the laboratory. These measurements were used to relate assimilation and growth efficiencies to larval age (and size) and prey ration level. Larval growth was 0.06 mm/d during the transition from endogenous to exogenous food (days 4–16), and increased to 0.16 mm/d (days 19–21). Ingestion ranged from 24 to 58% body dry weight/d. Oxygen consumption rates were measured and used to partition total daily metabolic expenditures into four components: resting metabolism; SDA; lights-on generated nonfeeding activity; and active (feeding) metabolism, which accounted for 45.7, 13.3, 11.1, and 29.9% of the total daily metabolic rate, respectively. Net assimilation efficiency ranged from 24 to 64% and gross growth efficiency ranged from 9 to 35%, depending on larval age and size. Little difference was observed in efficiencies at low and high ration levels. The daily caloric requirement to support metabolism and growth of first-feeding larvae was calculated at 0.16 calories, which is equivalent to 76 copepod nauplii. This value is higher than ingestion estimates from field studies.

Capture and transformation of energy into body mass is especially critical during the larval stage of marine fishes. Specific growth rate is highest during this stage and weight may increase by three orders of magnitude (Smith 1985; Houde 1987). Furthermore, duration of the larval stage, as regulated by growth rate, is recognized as a crucial factor in determining year class strength (Houde 1987; Miller et al. 1988). Growth efficiency, the proportion of ingested energy used in growth, depends on a number of factors including environmental conditions, prey quality, prey abundance, and larval size and age.

Walleye pollock, *Theragra chalcogramma*, is the most abundant commercial species in the northeastern Pacific Ocean, comprising 80% of the total groundfish catch (Bakkala et al. 1986). Several studies have evaluated the bioenergetics of late larvae, juveniles, and adults (Fukuchi 1976; Nishiyama 1981; Harris 1985; Smith and Paul 1986; Dwyer et al. 1987; Smith et al. 1988) but there are relatively few studies of bioenergetics of early larvae, and their growth efficiency is unknown. Incze et al. (1984) reviewed the early life history of this species and calculated daily ration based on literature-derived values of growth and respiration. Clarke (1984) made a similar estimate. Early studies of larval walleye pollock respiration were limited because larvae were not successfully grown in the laboratory. Likewise, estimation of larval growth, determined from otolith ageing, was limited by the lack of daily increment validation. Recently, walleye pollock larvae have been successfully reared in the laboratory (Bailey and Stehr 1986), and daily growth increments on otoliths have been validated (Nishimura and Yamada 1984; Bailey and Stehr 1988).

In the present study we estimate components of the energy budget of larval walleye pollock reared in the laboratory. These components include rates of ingestion, growth, and metabolism. Oxygen consumption was measured at different levels of activity in order to model daily metabolic costs. We also calculated efficiencies of assimilation and growth for larvae as influenced by ration and age.

MATERIALS AND METHODS

Rearing of Larvae

Experiments were carried out from March to May 1988. Eggs from ripe females, collected in Puget Sound, were fertilized and reared according to methods described by Bailey and Stehr (1986). Yolk-sac larvae were transferred to 120 L black fiberglass tanks set in a water bath. Initial stocking density was 1,200 larvae per tank. Overhead fluorescent lights, on a 14 h

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light:10 h dark cycle, illuminated the tanks at an intensity of 5–8 $\mu E/s/m^2$ just below the water surface. Water was replaced with filtered seawater at 10–15% per day. Larvae were fed rotifers, *Brachionus plicatilis*, that had been cultured on a mixture of *Isochrysis* spp., *Chaetoceros* spp., and yeast.

Three rearing experiments were done using larvae hatched from eggs collected on different days. In the first experiment, growth, rate of gastric evacuation, and daily ration were measured in larvae reared at high (11.2 ± 1.4 SD rotifers/mL) and low (2.0 ± 1.4 SD rotifers/mL) rations. Mean temperature in both tanks was 6.4°C (±0.2 SD). In the second and third experiments, oxygen consumption rates for larvae were determined. Rotifer densities were maintained at about 10 individuals/mL. Average temperature was 6.3° ± 0.1°C (SD). Temperatures of 6.0°–6.5°C are common in Shelikof Strait (Gulf of Alaska) in May when early-stage larval walleye pollock are most abundant (Kendall et al. 1987).

Growth Rates

The standard lengths (SL) of live larvae were measured to the nearest 0.03 mm using a dissecting microscope, the gut contents were removed, and the larvae were dipped in distilled water and then dried for 24 hours at 60°C. Dry weights were measured to the nearest 0.1 μg on a Cahn 25 electrobalance. Yolk-sac dry weight was estimated as the difference between the mean dry weight of larvae with yolk sacs and the mean dry weight of larvae whose yolk sacs had been excised. Instantaneous rate of growth (G) and relative rate of growth (K) were estimated from the following equations (Ricker 1975):

$$W_t = W_0\, e^{G \cdot t}, \text{ where}$$

$$G = (\ln W_t - \ln W_0)/t, \text{ and}$$

$$W_t = W_0(1 + K)^t, \text{ where}$$

$$K = e^G - 1.$$

W_0 is the initial dry weight (in μg) and W_t is the dry weight at time t (in days). Daily specific growth rate is defined as G (× 100%) (Laurence 1975).

In order to compare subarctic walleye pollock with the subtropical larvae used in other studies, we used methods and analyses to parallel those of Houde and Schekter (1981, 1983) and Theilacker (1987). One major difference was that we did not use nonfeeding larvae, but sampled randomly from feeding larvae. Theilacker (1987) used all randomly sampled larvae including nonfeeding larvae to estimate ingestion and growth; Houde and Schekter (1981, 1983) sampled only feeding larvae to measure ingestion, and feeding and nonfeeding larvae to measure growth. In some species, relatively few larvae may feed on cultured prey at low densities in laboratory conditions. This may not have been a problem in the Theilacker (1987) and Houde and Schekter (1981, 1983) studies. In our studies we considered feeding incidence as a behavioral problem not to be included as a factor in a study of energetic efficiency. Since our objective was to compare efficiencies of larvae feeding at high and low rations, we opted to exclude nonfeeding larvae from our samples.

Evacuation Rates

Instantaneous rates of gastric evacuation were measured for actively feeding larvae. Larvae were fed rotifers, dyed with Alcian Blue, at prey densities of 2.2–4.0/mL. After 1.2–1.5 hours larvae were transferred to a tank containing undyed rotifers either at 11.1–15.6 rotifers/mL for the high ration treatment or at 0.8–1.8 rotifers/mL for the low ration treatment. Larvae were sampled at intervals from 20 to 60 minutes, and widths of rotifers and their degree of digestion determined. Mean gut-clearance times were estimated for the duration between ingestion and defecation of dyed rotifers.

Theilacker and Kimball's (1984) method was used to determine that 54% of rotifer dry weight was lost after 4 hours of digestion. Based on that loss, three correction factors for the degree of rotifer digestion were used to calculate ingestion: 0.9 for recently ingested rotifers; 0.7 for moderately digested rotifers, which still had abundant chlorophyll from ingested phytoplankton; and 0.5 for well-digested rotifers with almost no chlorophyll. The total dry weight of dyed rotifers in the gut was determined by summing the product of the width-specific dry weight for each rotifer (Theilacker and Kimball 1984) and the appropriate digestion factor. Data were fitted to the model:

$$A_t = A_0\, e^{\,R \cdot t}$$

where A_0 and A_t are the ratios of the dry weight

of dyed rotifers in the gut to larval dry weight at times 0 and t (in hours). R is the calculated instantaneous rate of gastric evacuation.

Ingestion Rate

About 10 larvae from both high and low prey-ration tanks were sampled 5 times each day at 1.5–3 h intervals during the light period. Prey were removed from larval guts, counted, their widths measured, and the degree of larval digestion determined. Total gut content in dry weight per larva was determined by summing the product of the width-specific dry weights of rotifers and digestion factors.

Asymptotic curves of the form

$$S = S_{\max} \times (1 - e^{-F \cdot t}),$$

were used to describe ingestion rates, where S is the ratio of gut content to larval dry weight ($\times$ 100%) at time t (in hours) after initiation of light period, $S_{\max}$ is the asymptotic gut content (%) and F is the instantaneous rate of gut filling.

Weight-specific daily ration (I) as a percent of body weight was estimated for larvae using the Elliot and Persson (1978) model:

$$I = \sum_{i=1}^{m} (S_i - S_{i-1} e^{-R \cdot t_i}) R t_i / (1 - e^{-R \cdot t_i})$$

In this model, t_i is the duration of each time interval (i) in hours; S_i is the mean gut content at the end of interval (i) as a percent of larval dry body weight; and m is the total number of intervals during a light cycle. S_0 was assumed to be 0; and S_m, the gut contents at the end of the light period, was approximated as $(S_{m-1} + S_{m-2})/2$.

Metabolic Rates

Oxygen consumption rates were measured using the micro-Winkler technique (Carrit and Carpenter 1966; Strickland and Parsons 1972). We assumed that there are four metabolic activity levels: 1) resting or basal (M_{re}); 2) routine (M_{ro}), which includes M_{re} plus a cost for an lights-on generated activity; 3) feeding (M_{fn}), which includes M_{re} and an additional cost for specific dynamic action (SDA); and 4) active (M_a), which includes M_{re} plus increments due to lights-on activity and SDA, and an additional cost of pursuing and capturing prey.

Oxygen consumption rates for the different levels were measured as follows:

1. M_{re}: larvae were allowed to void their guts for 24 hours and were then incubated in dissolved oxygen (DO) bottles for 24 hours in complete darkness.
2. M_{ro}: larvae were allowed to void their guts for 24 hours and were incubated for 12 hours in the light during daytime.
3. M_{fn}: larvae with full guts after a 12 h feeding period were incubated for 12 hours in the dark during nighttime.
4. M_a: larvae with a few rotifers in their guts were incubated for 12 hours in the light during daytime with rotifers at a density of 5 individuals/mL.

Sixty milliliter DO bottles were used for conditions 1–3 and 300 mL DO bottles for condition 4. The bottles were set in a black container filled with seawater. Each bottle contained 5–30 larvae depending on larval and bottle size. Three to five replicates with control blanks (containing rotifers in condition 4) were carried out for each age and condition at 6.2 ± 0.1(SD)°C. Light intensity at the top of bottles was 6–9 $\mu E/s/m^2$ during the light period.

The value for M_{re} used here may be larger than that of other studies that use anesthetized larvae (Holliday et al. 1964; de Silva and Tytler 1973; Davenport and Lönning 1980; de Silva et al. 1986), as larvae normally move at night, even though at a much reduced level (Batty 1987). However, our method eliminates possible biases involved with the use of anesthetics. The active metabolism (M_a) was probably underestimated owing to restricted activity and feeding in 300 mL bottles, and to effects of handling. Restricted feeding in DO bottles was evidenced by the lower number of ingested rotifers in guts at the end of experiments compared with the number of ingested rotifers in the guts of larvae in the 120 L tank.

Energy Budget

Energy budgets (in calories per day) were determined for feeding larvae from 7 to 21 days from posthatching using the equation:

$$I = G + M + E$$

where I = ingestion, G = growth, M = metabolism, E = nitrogenous and fecal excretions. Excretion was not measured, but the total loss of

wastes can be estimated by difference. Also, the efficiencies we used—G/I, M/I, $(G + M)/I$, and $G/(G + M)$—are not dependent on excretion measurements.

Average daily ingestion in dry weight was calculated as (mean larval weight) × (weight-specific daily ingestion). Dry weight of rotifers was converted to caloric equivalents using a factor of 4.4 cal/mg (Theilacker and Kimball 1984).

Daily growth of larvae at (t_i) was calculated from the daily growth rate (K) for the interval $t_i - t_{i+1}$. Dry weight was converted to calories using a factor of 5.077 cal/mg estimated for larval walleye pollock (Fukuchi 1976; Harris et al. 1986). Fukuchi (1976) also provided constants for converting dry weight to net weight, nitrogen, and carbon (8.59, 0.092, and 0.131, respectively).

Daily O_2 consumption rate (M_{24}) μL/d/individual (14 h light and 10 h dark photoperiod) was calculated as

$$M_{24} = 2 \times (M_{ro}) \times 14 + (M_{fn}) \times 10.$$

Oxygen consumption was converted to calories using an oxycaloric equivalent of 4.63 cal/mL O_2 (Brett and Groves 1979). We attempted to measure active metabolic rates as described above, but larvae did not actively feed. Therefore, active metabolic rate was approximated as twice the routine metabolic rate (Houde and Schekter 1983; see also Lasker 1970).

RESULTS

Growth rates

Hatching began 7–8 days after fertilization, and by 3–5 days later more than 80% of the eggs had hatched. The day of 50% hatching was designated as the day of hatching for all larvae.

By day 6 after hatching, yolk-sac dry weight was less than 5% of the initial weight; the yolk was absorbed completely by days 11–15. A small percentage of larvae started feeding on day 5 and most larvae started on day 6. Therefore, day 6 was designated as the onset of feeding. Newly hatched yolk-sac larvae averaged 3.80 mm (SL) and 55.5 μg (dry weight), and by day 4 (existing only on yolk) averaged 4.59 mm and 47.5 μg. By day 21, high ration larvae grew to 6.02 mm (mean SL) and 120.9 μg (mean dry weight) and low ration larvae grew to 5.94 mm and 116.2 μg. The linear growth rate in SL during yolk-sac period (from days 0 to 4) was 0.20 mm/d; it decreased to 0.07 (high ration) and 0.06 (low ration) mm/d during the transition from endogenous to exogenous energy (from days 4 to 16), and then increased to 0.13 (high ration) and 0.12 (low ration) mm/d (from days 16 to 21). Specific growth rate in weight from days 7 to 21 was estimated as 6.71%/d for high ration and 6.04%/d for low ration larvae. Standard length (SL) and dry weight (W) were related by a power function:

$$\text{high ration: } W = 0.1261 \times \text{SL}^{3.812} \quad (r = 0.980 \quad N = 45)$$

$$\text{low ration: } W = 0.1754 \times \text{SL}^{3.615} \quad (r = 0.979 \quad N = 45).$$

Although the length-specific weight gain of high ration larvae tended to be greater than that of low ration larvae, the difference between the two food levels was not statistically significant (F-test for difference between two linear regression slopes, $P > 0.1$).

Evacuation Rates

The weight of dyed rotifers in larval guts decreased exponentially for the first 5–7 hours, then the rate of larval digestion slowed. Instantaneous rates of gastric evacuation (R) were estimated from the exponential phase for 8–9 d old larvae and 17–21 d old larvae. Rates for younger larvae were higher than those for older larvae, and high ration larvae had higher evacuation rates than low ration larvae (Table 1). The same tendencies were found in gut clearance times. Coiling of the midgut is initiated at about 5.2 mm SL (day 14) and is completed at about 5.8 mm (day 20), effecting the differentiation of foregut and intestine. The relationship between R and the percentage of larvae having coiled midgut (>5.5 mm SL) showed higher evacuation rates for larvae without the coiled gut.

Ingestion Rate

By our observation, larval walleye pollock are continuous feeders. There was no significant difference (Chi-square test: $P > 0.1$) between widths of rotifers in larval guts and widths of rotifers in cultures provided to larvae as food.

The ratio of gut contents to larval dry weight generally increased asymptotically with time (Fig. 1). Maximum mean percent of gut contents measured after 14 h feeding were 6.9% and 5.1% for 7 d old high ration and low ration larvae, respectively. These values increased to about 10% by day 13 and thereafter remained fairly

TABLE 1.—Instantaneous rates of gastric evacuation and gut clearance time related to age and feeding condition of larval walleye pollock at 6.4°C. Data were fitted to the equation: $A_t = A_0\ e^{-Rt}$ (see text). Also shown is the percent of larvae in the experiments greater than 5.5 mm SL, as an indicator of those with midgut coiling.

Age (d)	Feeding condition	Instantaneous evacuation rate (R)	A_0	Gut clearance time (h)	% Larvae >5.5 mm SL	N
8	high ration	0.473	3.399	5.3	0	93
9	low ration	0.415	2.571	6.1	0	97
17	low ration	0.263	2.601	10.1	64	61
18	high ration	0.256	3.082	9.6	79	61
21	high ration	0.327	4.743	9.4	73	40

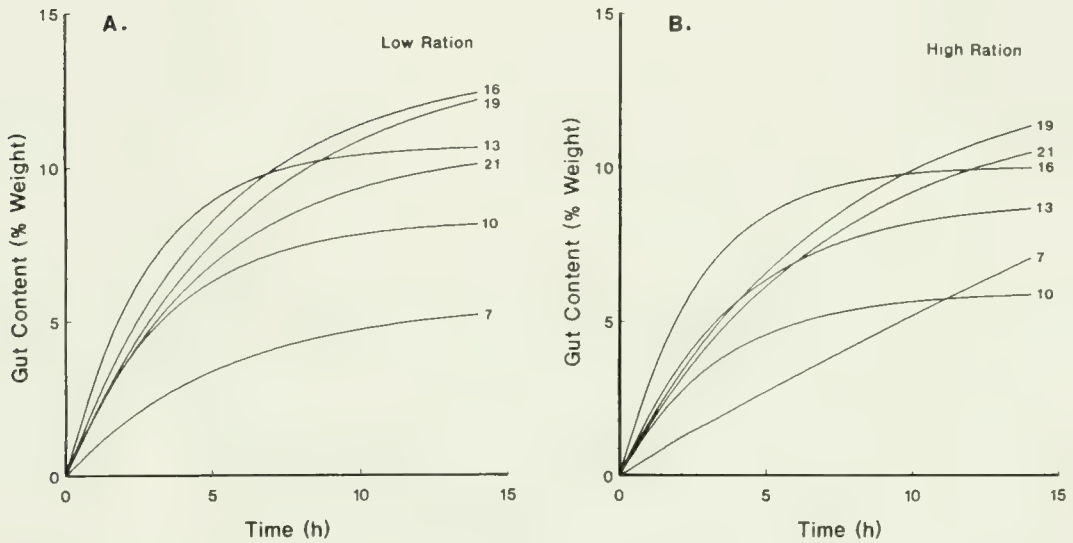

FIGURE 1.—Curves to describe food intake of low ration (A.) and high ration (B.) pollock larvae. Data were fitted to the equation: $S = S_{max} \times (1 - e^{-F \cdot t})$, where S is percent dry weight of gut contents to larval dry weight at time t (h) after initiation of light period; S_{max} is the asymptotic gut content (%); and F is the instantaneous rate of gut filling. Numbers after each line indicate age in days.

constant (Table 2). About 10–12% seems to be the maximum capacity of larval pollock guts within the range of stages examined. These measured maximum values are close to S_{max} values predicted from the asymptotic gut content curve (Table 2). The value for 7 d old high ration larvae was an exception; the ingestion curve appeared to be nearly linear and the resulting S_{max} high (Fig. 1; Table 2)

To estimate daily ration, instantaneous rates of gastric evacuation under specific age and feeding conditions were taken from Table 1. At day 7, one day after feeding commenced, weight-specific daily ration was low, about 24–29% (Table 2). Daily ration increased to a level of about 55% at days 13–16. In spite of the observed constant values of maximum percent gut contents with age, daily ration decreased to about 35% by day 21. The difference in daily ration between the high and low ration conditions was not significant (ANOVA, $P > 0.1$).

Metabolic Rates

Results of oxygen consumption rate measurements are summarized in Table 3. From day 0 to day 4 after hatching there was no remarkable difference in respiration between daytime (M_{ro}) and night (M_{re}). After day 6, when most larvae commenced feeding, O_2 consumption rate increased as age and weight of larvae increased, and M_{ro} was from 25 to 68% higher than M_{re}. O_2 consumption rates in the four conditions were significantly different (ANOVA, $P < 0.01$).

TABLE 2.—Summary of ingestion experiments for larval walleye pollock. S_{max} is estimated asymptotic gut content and F is instantaneous rate of gut filling. Parameters were estimated from the equation: $S = S_{max} \times (1 - e^{-Ft})$ (see text).

Diet	Age (d)	N	Asymptotic curve model: Instantaneous rate of gut filling (F)	Asymptotic[1] gut content (S_{max})	Estimated[1] gut content after 14 h feeding	Max mean gut content of reared larvae (%)	Daily ration (%)
High ration	7	30	0.017	33.5	7.1	6.9	29.4
	10	37	0.292	6.0	5.9	6.4	37.3
	13	41	0.250	9.0	8.7	9.8	50.9
	16	35	0.371	10.1	10.0	10.8	53.2
	19	40	0.138	13.3	11.4	11.2	42.1
	21	41	0.141	12.2	10.5	10.9	37.0
Low ration	7	32	0.185	5.6	5.2	5.1	24.2
	10	37	0.288	8.3	8.1	8.5	42.3
	13	41	0.362	10.7	10.6	11.0	58.5
	16	35	0.196	13.3	12.4	11.5	49.6
	19	40	0.162	13.6	12.2	11.3	38.1
	21	41	0.205	10.7	10.1	9.8	33.7

[1]Percent of gut content to larval dry weight.

TABLE 3.—Oxygen consumption rates at 6.2°C for larval walleye pollock at different experimental activity levels. The number of replicates per treatment was 3-5. Values in parentheses are for yolk-free weights.

Age (d)	Mean dry weight (μg)	Oxygen consumption activity level: Resting (M_{re}) μL/h/ind	SD	μL/h/mg	Routine (M_{ro}) μL/h/ind	SD	μL/h/mg
0	54.2	0.068	0.011	1.25(2.06)	0.068	0.003	1.26(2.08)
3	53.1	0.082	0.008	1.55(1.89)	0.086	0.019	1.61(1.96)
4	48.3	0.076	0.004	1.58(1.72)	0.077	0.012	1.59(1.76)
6	47.6	0.083	0.008	1.74(1.76)	0.112	0.019	2.35(2.38)
11	55.1	0.098	0.009	1.78	0.123	0.037	2.24
14	68.1	0.104	0.026	1.53	0.140	0.023	2.06
19	87.9	0.129	0.021	1.47	0.217	0.064	2.47
20	89.8	0.137	0.030	1.53	0.226	0.022	2.52
23	131.3	0.212	0.026	1.61	0.269	0.051	2.05

Age (d)	Mean dry weight (μg)	Oxygen consumption activity level: Feeding (M_{fn}) μL/h/ind	SD	μL/h/mg	Active (M_a) μL/h/ind	SD	μL/h/mg
6	47.6	0.100	0.014	2.09(2.12)	0.136	0.016	2.87(2.91)
11	55.1	0.134	0.024	2.43	0.153	0.042	2.78
14	68.1	0.134	0.017	1.97	0.193	0.036	2.83
19	87.9	0.153	0.026	1.74	0.251	0.036	2.86
20	89.8	0.185	0.020	2.06	0.304	0.008	3.39
23	131.3	0.287	0.067	2.19	0.406	0.074	3.07

The relationships of O_2 consumption rate (μL/h/individual) and mean larval dry weight (W, in μg) of feeding larvae for the different metabolic levels were

$$M_{re} = 0.00276\, W^{0.8707} \quad (r = 0.844,\ n = 26)$$
$$M_{ro} = 0.00253\, W^{0.9699} \quad (r = 0.807,\ n = 27)$$
$$M_{fn} = 0.00308\, W^{0.9059} \quad (r = 0.845,\ n = 25)$$
$$M_{a} = 0.00176\, W^{1.1154} \quad (r = 0.906,\ n = 25)$$

The metabolic mass exponents, particularly for routine metabolism, were close to unity.

For prefeeding larvae, weight-specific O_2 consumption rate (μL/h/mg) increased with age (Table 3). This is probably associated with increasing somatic tissue, because yolk is thought to be nonrespiring (Rombough 1988). Weight-specific rates, using yolk-free dry weight, decreased with age. As the eye became functional, at days 5 and 6, a rapid rise in routine metabolism followed the increase in light-stimulated activity. From days 6 to 23 there were no significant trends in the dry weight specific O_2 consumption rate with age for any treatments (ANOVA with regression, $P > 0.1$).

By difference ($M_{ro} - M_{re}$), lights-on generated activity of feeding larvae accounted for an average O_2 consumption of 0.67 μL/h/mg. Nighttime SDA ($M_{fn} - M_{re}$) accounted for 0.47 μL/h/mg, and feeding activity associated with hunting and capture of prey ($M_a - M_{ro} - 0.47 - 0.67$) accounted for 0.22 μL/h/mg. Given that the active-feeding metabolic rate was probably underestimated by our technique as noted previously, and that the active metabolic rate can be estimated as $2 \times M_{ro} = 4.56$ μL/h/mg, the above increment for active metabolism would be 1.81 μL/h/mg.

Energy Budget

Energy budget components and efficiencies are given in Table 4. Gross growth efficiency ($G/I \times 100$) ranged from 13.2 to 34.5% for high ration and from 9.1 to 32.6% for low ration larvae. The relationship of G/I and age was a U-shaped function with low efficiency in middle stages (Fig. 2). The ratio of metabolizable energy to ingestion ($(G + M)/I \times 100$) is termed net assimilation efficiency. Net assimilation efficiency also showed a U-shaped relationship with age, ranging from 30.5 to 58.4% and from 24.4 to 63.5% for high ration and low ration larvae, respectively. The ratio of the growth component to metabolizable energy ($G/(G + M) \times 100$) gradually increased from 40-42% at day 7 to 55-59% at day 21.

DISCUSSION

The growth rates of walleye pollock larvae in our experiments compared favorably to those of

TABLE 4.—Daily energy budget components and efficiencies of larval walleye pollock. H and L indicate high ration and low ration levels, respectively.

Age:	7	7	10	10	13	13	16	16	19	19	21	21
Feeding condition	H	L	H	L	H	L	H	L	H	L	H	L
Mean SL (mm)	4.77	4.81	4.94	4.96	5.13	5.15	5.38	5.35	5.71	5.69	6.02	5.94
Mean dry weight												
(W_D)(μg)	46.5	48.6	54.0	57.3	67.6	68.4	80.2	78.1	98.0	96.6	120.9	116.2
(cal)[1]	0.236	0.247	0.274	0.291	0.343	0.347	0.407	0.397	0.498	0.492	0.614	0.590
Ingestion (I)												
(μg/d)	13.66	11.75	20.14	24.26	34.43	40.00	42.67	38.73	41.28	36.95	44.67	39.16
(cal/d)[2]	0.060	0.052	0.089	0.107	0.151	0.176	0.188	0.170	0.182	0.163	0.197	0.172
Growth (G)												
(μg/d)[3]	2.37	2.72	4.21	3.50	3.99	3.08	5.53	5.86	10.88	9.21	13.42	11.04
(cal/d)[2]	0.012	0.014	0.021	0.018	0.020	0.016	0.028	0.030	0.055	0.047	0.068	0.056
Metabolism (M)												
(μL O_2/d)	3.94	4.11	4.57	4.85	5.72	5.79	6.79	6.61	8.29	8.29	10.23	9.84
(cal/d)[4]	0.018	0.019	0.021	0.022	0.026	0.027	0.031	0.031	0.038	0.038	0.047	0.046
G/I[5] (%)	20.0	26.9	23.6	16.8	13.2	9.1	14.9	17.6	30.2	28.8	34.5	32.6
M/I[5] (%)	30.0	36.5	23.6	20.6	17.2	15.3	16.5	18.2	20.9	23.3	23.9	26.7
$(G + M)/I$[5] (%)	50.0	63.5	47.2	37.4	30.5	24.4	31.4	35.9	51.1	52.1	58.4	59.3
$G/(G + M)$[5] (%)	40.0	42.4	50.0	45.0	43.5	37.2	47.5	49.2	59.1	55.3	59.1	54.9
I/W_D[5] (%)	25.4	21.1	32.5	36.8	44.0	50.7	46.2	42.8	36.5	33.1	32.1	29.2

[1]Larval dry weight was converted to calories by a factor of 5.077 cal mg^{-1}.
[2]Rotifer dry weight was converted to calories by a factor of 4.4 cal mg^{-1}.
[3]Daily growth was calculated using the relative rate of growth (K) at each day interval.
[4]Oxygen volume was converted to calories by a factor of 4.63 cal mL^{-1} O_2.
[5]Efficiencies were expressed on caloric basis.

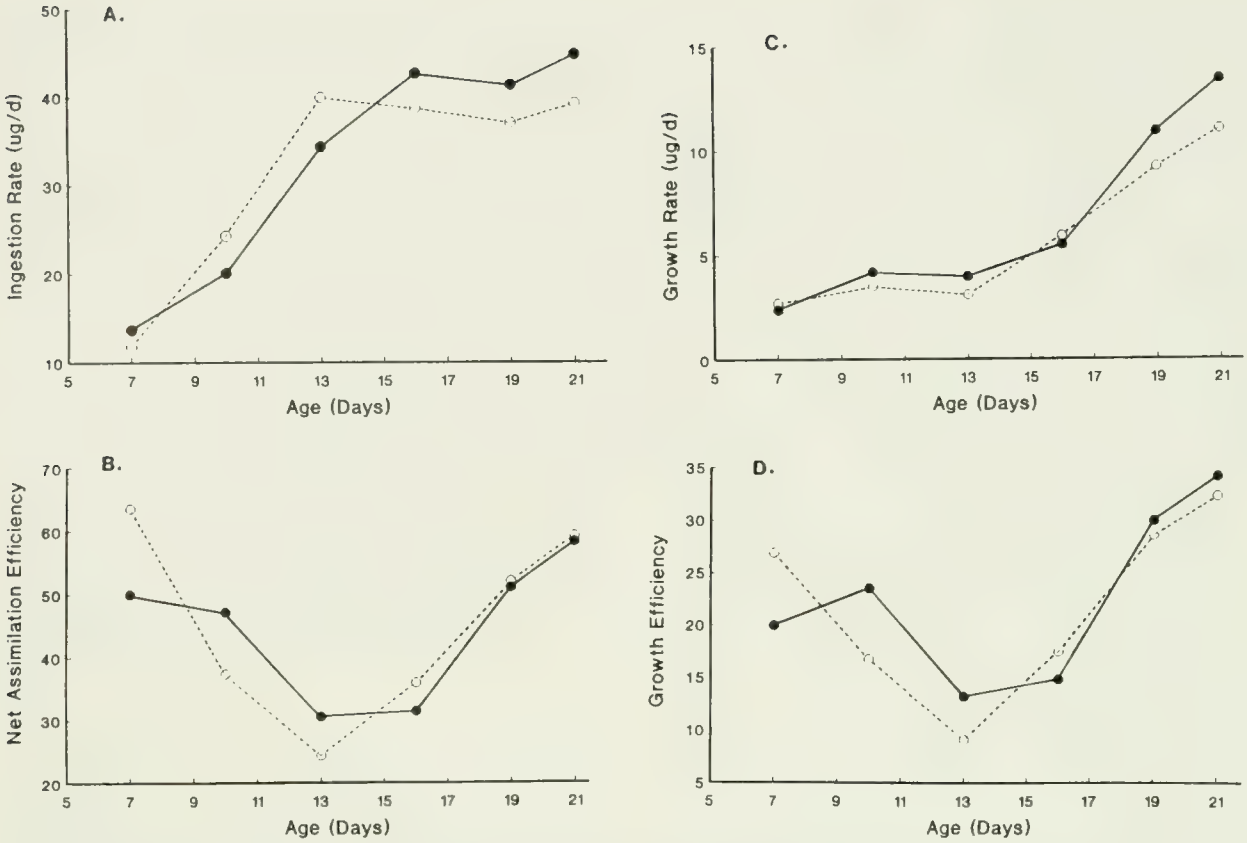

FIGURE 2.—Ingestion rates (A.); net assimilation efficiencies (B.); growth rates (C.); and growth efficiencies (D.) of reared walleye pollock larvae. Closed circles and open circles indicate well fed and poorly fed larvae, respectively.

larvae caught at sea. In the laboratory, yolk-sac larvae from days 0 to 4 (posthatch) were growing 0.20 mm/d at 6.4°C. Growth rates decreased to 0.06 mm/d just after onset of feeding (4.8 mm SL) and increased to 0.16 mm/d from days 19 to 21 (5.8 mm SL). Growth rates of field-collected walleye pollock larvae, determined from otolith increments, ranged from 0.12 to 0.25 mm/d, linearized over ages 7–45 days (6.0–14.6 mm SL) for larvae caught in the Gulf of Alaska in 1983 (at 5.5°–7.0°C (Kendall et al. 1987)). In 1987 the growth rate of Gulf of Alaska walleye pollock larvae at 5.8 mm SL was 0.18 mm/d as determined from the growth equation given in Yoklavich and Bailey (1989). Growth of field-caught larvae, like laboratory-reared larvae, was slow at ages corresponding to the transition from endogenous to exogenous feeding. Specific growth in dry weight was 7%/d. This is somewhat slower than the wet weight-specific growth rates estimated from field-caught larvae at 10%/d (Fukuchi 1976; Nishiyama 1981). These weight-specific growth rates are much lower than those of subtropical species (from 15 to 50%/d) (Houde and Schekter 1983; Theilacker 1987), but they are similar to those of other subarctic species (Laurence 1975; 1978)

Decreased evacuation rates with increased larval size (and age) were closely related to the development of the digestive system, especially midgut coiling, which begins at about 5.2 mm SL (13–16 days) and is completed at about 5.8 mm (19–21 days). Our gut clearance times (5.3–6.1 hours) for first-feeding larvae fed rotifers are similar to the 5 hours found by Paul (1983) for pollock larvae fed copepod nauplii at 5.5°C. Generally these gut clearance times are considerably slower than those of warm-water species, e.g., northern anchovy at 1.15–1.5 hours (Theilacker 1987). Walleye pollock larvae with high ingestion rates in high prey densities had faster rates of gut clearance compared with those held in low prey densities. Furthermore, larvae with full guts placed in prey-free water had very slow clearance rates, indicating that continuous feeding facilitates movement of ingested prey through the guts.

Specific daily ration increased from 21 to 25% at day 7 to a peak value of 46-51% at days 13–16 as a function of increasing ingestion rates. It

declined to 29–32% at day 21 as a result of the longer gut clearance times discussed previously. The inverted U-shaped function observed here was also noted by Houde and Schekter (1981) while studying three species of subtropical larvae. Daily rations for warm-water species are considerably higher than those found in this study, ranging from 202 to 379%, 165 to 297%, and 121 to 234% per day on a caloric basis for bay anchovy, *Anchoa mitchilli*, lined sole, *Achirus lineatus*, and sea bream, *Archosargus rhomboidalis*, respectively (Houde and Schekter 1983); values of 26–70% were found for northern anchovy converted to a caloric basis from data in Theilacker (1987); and values of 42–160% on a dry weight basis for summer flounder, *Paralichthys dentatus*, (Buckley and Dillmann 1982).

Our values of routine metabolism at 6.2°C in Table 4 correspond quite closely to values for walleye pollock and cod found by other investigators. For example, our values of 2.24 and 2.06 μL/h/mg for 11 and 14 d old larvae are similar to values of 1.86 and 2.14 for 11 and 14 d old pollock larvae at 4°C found by Clarke (1984). Adopting a Q_{10} value of 2.3 (Brett and Groves 1979), Clarke's values are equivalent to 2.23 and 2.57 μL/h/mg at 6.2°C. Routine metabolic rates for young cod larvae at 5°C have been measured at 1.6 (Davenport and Lönning 1980) and at 1.8–2.0 μL/h/mg (Solberg and Tilseth 1984).

We attempted to partition metabolism into its component parts for estimating daily metabolic cost. From the equation for total daily metabolism, the four components—SDA, lights-on generated nonfeeding activity, resting metabolism, and feeding activity—accounted for 13.3, 11.1, 45.7, and 29.9% of the total daily metabolic expenditure. Because of the experimental nature of these measurements, they should be considered a first approximation, subject to refinement. For example, degradation of rotifers that were defecated in the DO bottles could have consumed some of the available oxygen and should be controlled for in future studies. Our values for resting metabolism may include some cost for biosynthesis because a 24 h period of nonfeeding acclimation time is probably not enough to eliminate the effect of SDA (Brett and Groves 1979). The value for active feeding metabolism seems high compared with the relatively inactive behavior of walleye pollock larvae. The assumption that active metabolic rate is twice the routine metabolic rate may have resulted in an overestimate of this component.

Net assimilation efficiency [$(G + M)/I$], ranged from 24 to 64% in our study, as a U-shaped function related to age. These efficiencies are low compared with generalized rates of 65–75% for young fish given by Ware (1975) and 73% for young carnivorous fish given by Brett and Groves (1979). However, the assimilation rate during larval life seems to change greatly during development, and rates are usually quite low for young larvae. For example, net assimilation efficiency for northern anchovy changed with increasing larval size from 44.4 to 65.7% for well-fed larvae (Theilacker 1987). Net assimilation efficiency for bay anchovy, lined sole, and sea bream ranged from 17.2 to 33.7%, 26.6 to 46.1%, and 37.2 to 67.6%, respectively, for different developmental stages of these fishes (Houde and Schekter 1983).

High assimilation efficiency during the first few days of feeding may be due partly to residual yolk contributing to "ingestion". Yolk is converted into body tissue very efficiently (Lasker 1962). Assimilation efficiency decreased to a low point at day 13 of our experiments. We suggest that development of the digestive system lagged behind that of behavioral feeding prowess, and that low assimilation efficiencies were linked to the growth lag observed during the transition from endogenous to exogenous food. Assimilation efficiency and growth rate increased when ingestion reached a maximum and the alimentary canal developed midgut coiling, resulting in longer gut clearance time.

Gross growth efficiency (G/I) ranged from 11 to 34% as a U-shaped function of age (and size). Houde and Schekter (1983) reported similar U-shaped functions with size ranging from 10.9 to 20.8% for bay anchovy, from 12.8 to 23.3% for lined sole, and from 21.4 to 41.3% for sea bream. Most values for larvae are suggested to be in the 5–40% range (Houde and Schekter 1983) or 14–41% range (Theilacker and Dorsey 1980). The efficiencies of pollock larvae are consistent with these ranges. Our gross growth efficiencies are lower than those of 30–47% found by Theilacker (1987) for well-fed northern anchovy larvae.

Growth rates, ingestion rates, assimilation efficiencies, and growth efficiencies determined from this study differed surprizingly little between high and low rations. These results indicate that larvae robust enough to successfully initiate feeding at low prey densities were able to maintain high rations, and furthermore that growth responded very little to increased prey density. Lower levels of ration used here may be

necessary to assess the influence of marginal feeding conditions on growth or assimilation efficiency. Although we did not monitor feeding incidence and survival closely, both were higher in the high ration treatments. Consequently, including nonfeeding larvae in our study probably would have made differences appear in growth and ingestion rates between ration levels. Paul (1983) found fairly high incidences of pollock larvae feeding at low densities on copepod nauplii; however, the extreme smallness (250–1,000 mL) of containers used in that study probably invalidates the results.

According to Nishiyama and Hirano's (1985) formula for estimating mean gut content as a percent of wet body weight, guts of field-caught larvae 6 mm in total length (TL) should contain about 2% body weight. By contrast, larvae in our experiments contained 10–12% dry body weight. These results would indicate that either larvae in the field are not consuming prey at maximum rates, or there is a problem with collecting larvae from the field. Pollock larvae could be defecating when captured with nets; however, we observed that walleye pollock larvae did not defecate when probed with a dissecting needle, in contrast to anchovy larvae (Yamashita in press).

We can approximate mean caloric consumption of pollock larvae caught in the Bering Sea from the data of Dagg et al. (1984), who estimated that at an average temperature of 4.5°C, larvae 5.2 mm in length ingest 18.3 copepod nauplii/d. The mean length of copepod nauplii eaten by pollock larvae (5.2 mm TL) is 0.22 mm, as estimated from equations given by Nishiyama et al. (1986), and an equivalent wet weight is 1.38 μg (Nishiyama and Hirano 1985). Assuming 70% water content (Ikeda 1970) and the caloric content of adult *Pseudocalanus* (Laurence 1976), the mean caloric content of the average naupliar prey would be 0.0021 calories. Daily ingestion of larvae in the study of Dagg et al. (1984) would be 0.038 calories. Assuming 50% assimilation efficiency, 0.019 calories are available for metabolism and growth. This value, however, does not meet even the daily caloric requirement of 0.023 calories for metabolism alone, at 4.5°C (converted from 0.027 calories for metabolism of 13 d old larvae, 5.1–5.2 mm SL, at 6.2°C with an assumption of $Q_{10} = 2.3$ from Brett and Groves 1979). A daily caloric ingestion of about 0.16 calories is required for growth and metabolism for this size of larva from the results of our study. This value would be equivalent to 76 nauplii. Of course, prey size and metabolizable energy content may vary significantly.

The mean number of copepod nauplii at the depth of their maximum abundance in the Bering Sea during normal first-feeding of pollock larvae is 10–20/L (Clarke 1984; Dagg et al. 1984). These values are low compared with previously reported ranges of naupliar densities in the sea (e.g., Houde 1978; Hunter 1981). We believe that the low prey density, low percentage of gut contents to body weight of field-caught larvae, and the energetic requirements of larvae compared with estimated ingestion rates from field studies indicate that pollock larvae, like anchovy (Lasker 1975), are probably subject to food shortages in the sea. Since the growth response of walleye pollock larvae (at the low temperatures used in this study and in the sea) is low, one would not expect to see periodic episodes of low ration expressed markedly in mean larval growth rates (Yoklavich and Bailey 1989), but episodes of low ration would be better assessed on an individual basis, using chemical or histological methods.

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Size-Specific Vulnerability to Predation and Sensory System Development of White Seabass, *Atractoscion nobilis*, Larvae

Daniel Margulies

ABSTRACT: The size-specific vulnerability of white seabass, *Atractoscion nobilis*, larvae (2.5–15.0 mm SL) to two types of fish predators—adult northern anchovy, *Engraulis mordax*, and juvenile white seabass—was examined in laboratory predation trials. Concurrent analyses were made of the developmental ontogeny of larval visual and mechanoreceptive systems. The proportion of larvae responding to or escaping attacks by either predator increased with larval size. There were no significant differences in proportions of larvae responding to or escaping attacks of either predator until larvae were 6.0–7.5 mm SL (early postflexion stage). At this size, larvae were better able to evade the slower, more discontinuous attacks of juvenile white seabass compared with the faster attacks of adult anchovy. Major developmental events occur during this larval stage, including rapid improvement in visual acuity, visual accommodation to distant objects, growth and stratification of the optic tectum, and large increases in the numbers of free neuromasts on the head and trunk. It is likely that at larval sizes >7 mm SL, the slower attacks of juvenile white seabass allow more time for larvae to process and integrate visual and mechanoreceptive sensory input from several modalities. White seabass larvae (and sciaenids in general) become more demersal in distribution during the late larval stages in nearshore southern California waters. This ontogenetic shift deeper into the water column may be related to predator-avoidance capabilities of the larvae, since most demersal planktivores exhibit some type of hovering, ambush, or discontinuous mode of predation similar to that of juvenile white seabass and attack at much slower speeds than pelagic, shoaling fish predators. As they shift downward, older white seabass larvae may maximize their predator-detection capabilities when encountering demersal fish predators.

For most marine and estuarine fishes, predation-induced mortality during early life stages may be crucial in determining year-class strength. Predation has long been recognized as an important potential regulatory mechanism in prerecruit life stages (Houde 1978, 1987; Hunter 1981, 1984), but many of the specific factors that influence predation rates on early life stages are not well understood (Bailey and Houde 1989).

One of the crucial aspects of predator/prey dynamics involves the developmental or physiological basis for capture and escape responses. Fish larvae possess several sensory systems presumed to be important in predator detection; these include visual, mechanoreceptive, and auditory systems. During early ontogeny, these sensory systems undergo rapid development, and the improvement in these systems is thought to be crucial in controlling vulnerability to predation (Hunter 1984; Blaxter 1986). However, experimental investigations combining the study of larval sensory system development and vulnerability to predation are limited. Larvae of several species, including the northern anchovy, *Engaulis mordax*, (O'Connell 1981; Webb 1981; Folkvord and Hunter 1986), Atlantic herring, *Clupea harengus harengus*, (Blaxter et al. 1983; Blaxter and Batty 1985; Fuiman 1989), Cape anchovy, *Engraulis capensis*, (Brownell 1985), bloater, *Coregonus hoyi*, (Rice et al. 1987), and white perch, *Morone americana*, (Margulies in press) have been studied to examine either sensory system development or predator-avoidance behaviors. Similar studies have been conducted on larvae of flatfish (Neave 1984, 1986) and several gadoids (Fridgeirsson 1978; Bailey 1984). These types of investigations, however, have not been combined during one study using a single cohort of experimental fishes.

The purpose of this study was to examine, experimentally, the size-specific vulnerability of white seabass, *Atractoscion nobilis*, larvae to different types of fish predators, and to determine if there was a developmental or neurological basis for any observed changes in larval vulnerability or behaviors. The developmental studies of larval white seabass centered on the ontogeny of two sensory systems, vision and

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mechanoreception, which are presumed to be important components of predator detection and larval escape responses (Blaxter 1986). The ontogeny of avoidance/escape responses and other larval behaviors of white seabass were then analyzed in relation to the structural and functional development of their sensory systems.

Very little is known of the early life history of the white seabass, even though it is the largest sciaenid occurring in coastal waters of California and Baja California and has historically been a favored sport and commercial species (Feder et al. 1974; Vojkovich and Reed 1983). White seabass spawn in spring and early summer in nearshore coastal waters of southern California, and produce pelagic eggs. Abundance and distribution of young-of-the-year in southern California waters have been reported by Allen and Franklin (1988). Larval morphological development has been described by Moser et al. (1983), but larval ecology, predator-avoidance behaviors, and sensory system development have not been described.

METHODS

Larval Rearing

White seabass larvae used in the experiments were hatched from eggs obtained from broodstock adults maintained at the Hubbs Marine Research Center at Sea World in San Diego. Eggs were transported to the aquarium at the Southwest Fisheries Center La Jolla Laboratory and stocked in 76 L aquaria at stocking densities of 6 L^{-1}. During the culture experiments water temperature ranged from 17° to 19°C, and a constant photoperiod of 13 h light: 11 h dark was maintained.

First-feeding white seabass larvae were fed rotifers, *Brachionus plicatilis*, cultured on the green alga *Tetraselmis*. Older larvae were sequentially fed diets of *Artemia* nauplii, a mixture of *Artemia* nauplii and wild copepods, and adult *Artemia*. The developmental size range of white seabass tested ranged from hatching (2.6 mm SL, 0 day after hatch) to juvenile metamorphosis (15.0 mm SL, 42 days after hatch) (Fig. 1).

Experimental Predators

Adult northern anchovy and juvenile white seabass were used as predators. Both of these predator groups occur in nearshore waters of southern California and are potential natural predators of white seabass larvae. These two predator groups represent different types of raptorial predatory behavior (Table 1). Adult northern anchovy are pelagic, cruising predators that attack prey at relatively high speeds and often from oblique angles. Juvenile white seabass attack at much slower speeds and have a somewhat discontinuous mode of attack that involves an approach, glide, and then engulfing of prey. Northern anchovy also initiate attacks from much greater distances.

Predators were held in laboratory holding tanks and fed adult *Artemia*, minced euphausiids and occasionally white seabass larvae. To minimize predator learning behavior, after completion of predation trials on a given date, predators were transferred to separate holding tanks; this ensured that no predator was used more than twice during the 6 wk experimental period.

Experimental Methods

The predation experiments were conducted following the methods of Folkvord and Hunter (1986), with several modifications. Predation trials were carried out in rectangular fiberglass tanks, 1.4 m^3 in volume, with a clear glass win-

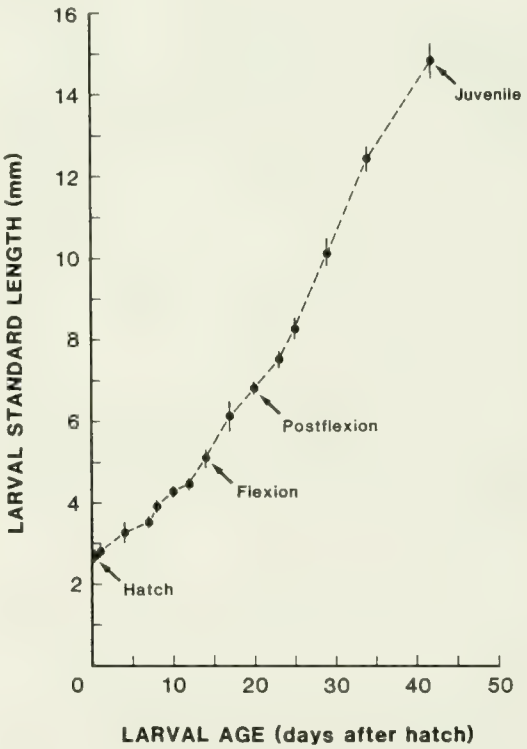

FIGURE 1.—Sizes, ages, and developmental stages of larval white seabass prey used in predation trials.

TABLE 1.—Modes of predation exhibited by adult *Engraulis mordax* and juvenile *Atractoscion nobilis*.

Predator	Size (mm)		Attack distance (dm)		Attack speed range (m/s)	Mode of attack
	Range	Mean	Range	Mean		
Engraulis mordax (Adults)	85–107	96.4	20–70	36.6	0.50–1.50	Fast speed; approach and attack continuous; often from oblique angle
Atractoscion nobilis (Juveniles)	62–86	72.2	5–30	14.7	0.05–0.20	Slow to moderate speed; attacks often discontinuous, with approach, glide, then ingestion; angle of attack horizontal or oblique

dow on one side for observation. Flourescent lamps produced 2,000–3,000 mc at the surface of each tank. A black plastic tent enclosed the window, providing a darkened compartment for observations. Metric rules placed on the tank window allowed estimation of predator attack distances. The tanks were supplied with flow-through ambient seawater (17°–19°C), except during an experiment when the water was static. Since adult northern anchovy often occur in large schools and juvenile white seabass are solitary or found in loose aggregations, it was decided that northern anchovy predators in groups of five individuals and white seabass in groups of three should be used. This simulated the predators' natural condition yet prevented predator "swamping" of larval prey.

Feeding motivation of predators was standardized by presenting constant numbers of adult *Artemia* to predators prior to predation trials with larvae. (*Artemia* are a good standard prey because they do not avoid predatory attacks by fishes.) Preliminary experiments had indicated that feeding behavior of adult northern anchovy was more variable than that of juvenile white seabass; thus, five groups of five *Artemia* each were presented to each anchovy predator group and three groups of five *Artemia* each were presented to white seabass. After the *Artemia* additions, white seabass larvae were introduced into the predation tanks in groups of five (each larval group added = trial). Trial duration was 10 minutes or until all prey were eaten. Larvae and *Artemia* were added to the tanks in clear beakers that were gently submerged at the water surface. After the initial *Artemia* trials, each predator group was tested with 6–8 larval trials, followed by a final *Artemia* trial to test for predator satiation.

On the same day as predation experiments, subsets of 10–12 larvae were removed from culture tanks and fixed in 5% formalin for calculation of mean larval sizes; additional subsets of larvae were removed for examination of sensory system ontogeny (discussed below). The total number of predator-prey interactions observed for each larval size class and predator type is presented in Table 2.

TABLE 2.—The total number of predator-prey interactions observed for each larval size and age class and predator type.

$\bar{x}$ larval size (mm)	Larval age (d)	Observations per predator type	
		Northern anchovy	White seabass
3.1	4	36	39
4.5	12	35	32
6.1	17	33	38
7.4	23	30	37
9.1	27	40	38
12.5	34	38	40
14.8	42	42	50

Classification of behaviors followed Folkvord and Hunter (1986). Four measures of predator-prey interactions were calculated: mean and maximum attack distances; percentage of larval avoidance responses; percentage of larval escapes; and predation rate (percentage of larvae captured during each 10 min trial). Approximate predator attack speeds also were estimated. A predator attack was a directed movement toward a prey with the mouth open. Predator attack distance was the distance in decimeters (dm) from a prey to the point of origin of attack. An avoidance response was a change in speed or direction of a larva occurring before a predator could complete an attack. An escape occurred when a predator failed to capture a larva during a single attack. Repeated attacks were scored as separate events.

Two potential biases to the predator-prey

interactions were addressed. Variation in predator performance was examined by calculating the percentage of predator error occurring in five groups of both types of predator feeding on adult *Artemia*. Since *Artemia* show no avoidance responses, a predator error was recorded when a predator simply missed the prey. Percentage of predator error was calculated for each predator group and among groups. In addition, potential stress or mortality of larvae due to handling was examined. For each larval size class, four replicates (trials) of five larvae each were transferred into 76 L tanks containing no predators. Mortality observed in control tanks was used to adjust for handling-induced mortality or increased vulnerability of larvae in predation trials.

Analysis of Larval Sensory System Development

Subsets of larvae from each size class were removed from culture tanks for analyses of larval visual and mechanoreceptive systems. Groups of 6–8 larvae from each size class were fixed in 5% phosphate-buffered formalin for histological analysis of organogenesis. Larvae were dehydrated, cleared, embedded in paraplast, and serially sectioned at 5 μm transversely and sagittally. Sections were stained with Harris' haemotoxylin, counterstained with eosin, and viewed under light microscopy at 80–1250 magnification. Ontogenetic development of the lens, retina, and optic tectum were examined and swimbladder inflation was noted. Size-specific visual acuity was calculated from retinal sections using the formula: $\sin \alpha = c/f$, where α is the minimum separable angle, c is the distance between the centers of adjacent cones, and f is the focal length of the lens (Neave 1984). Cones were measured as numbers per 100 μm length of retina (d), thus the reciprocal 10 d gives cone separation in mm. The expression was multiplied by 1.11 to adjust for approximate 10% shrinkage during processing, and the focal length of the lens was calculated by multiplying its radius (r) by 2.55 (Matthiessen's ratio; Matthiessen 1880), giving: $\sin \alpha = 0.0435/dr$.

Separate groups of 6–8 larvae from each size class were examined for development of free neuromast organs. These larvae were anaesthetized with MS-222 and immersed in a bath of the vital stain Janus Green (0.05% Janus Green made up with 50% seawater) (Blaxter et al. 1983). Larvae were immersed for 20–30 minutes and then removed for examination of number and location of free neuromasts under light microscopy.

Histological sections also were examined to determine the timing of swimbladder inflation in larvae.

Data Analysis

For each predation trial, predation rate (percent killed in 10 minutes) was calculated from the equation: $A = m + n - mn$, where A = total mortality rate, m = control mortality rate, n = experimental predation rate, and mn = the interaction effect which estimates the proportion of larvae consumed but which would have died anyway from handling stress or other causes (Ricker 1975). Percentage of larvae responding and escaping were considered total survival rates (S) and were calculated by first estimating total conditional mortality (A) (proportion "not responding" or "not escaping") and then calculating the difference as $S = 1 - A$ (Ricker 1975).

Lens diameter, visual acuity, and thickness of the optic tectum were calculated for each larval size class and developmental stage. Developmental ontogeny of the retina, optic tectum, and swimbladder were described. The mean number of neuromast organs also was calculated, and composite maps were developed of the patterns of neuromast organ formation.

Statistical analyses of data were performed using SAS (SAS 1982) statistical programs.

RESULTS

Predator/Prey Interactions

Potential Biases

Preliminary determinations of predator error by both predator types indicated that predator performance would not bias results. Mean predator error per trial for northern anchovy adults feeding on *Artemia* was 3.3% (range 2.1–5.1%) while error rate for juvenile white seabass was 2.7% (range 0.8–6.1%). There were no significant differences in mean error rate among predator groups, within trials, or between species (ANOVA, $P > 0.10$).

Larval mortality in control tanks (no predators) was low, ranging from 0.0 to 12.5% mean values for any larval size group. Experimental predation and escape rates were adjusted by the control rates.

Larval Responses

The probability of a white seabass larva responding to or escaping a predatory attack generally increased with larval size, although major differences in these responses were apparent depending upon type of fish predator. The mean percentage of larvae escaping attacks by northern anchovy ranged from 3% in yolk-sac larvae (3 mm SL) to 43% in metamorphosing fishes (15 mm SL) (Fig. 2A), while the percentage responding to anchovy attacks ranged from 14% (yolk-sac stage) to 56% (at metamorphosis) (Fig. 2B). Mean predation rate (percentage of larvae eaten in 10 minutes) by anchovy predators decreased from 95% on yolk-sac larvae to 56% on early juveniles (Fig. 2A). The predator/prey interactions were best described by exponential regressions (Fig. 2).

White seabass larvae were better able to respond to or escape attacks of juvenile white seabass than those of northern anchovy. Mean percentage of larvae escaping white seabass attacks ranged from 8% for yolk-sac larvae to 74% for metamorphosing fishes (Fig. 3A), while the percentage responding to attacks increased from 18% (yolk-sac stage) to 84% (at metamorphosis) (Fig. 3B). Responses and escapes from juvenile white seabass improved significantly in larger larvae, particularly between the larval sizes of 7.5 versus 9.0 mm SL (t-test, $P < 0.01$). Response and escape success nearly doubled during this developmental stage. Mean predation rate by juvenile white seabass predators decreased from 80% on yolk-sac larvae to 65% on 6 mm larvae, increased to 87% on 7.5 mm larvae, and then steadily decreased to 30% on early juveniles (Fig. 3A). These predation functions also were fit to exponential regressions (Fig. 3).

The success of avoidance movements by responding larvae (numbers escaping/numbers responding) generally increased with larval size (Table 3). Approximately 21% of responding larvae in the 3.1 mm size category successfully escaped northern anchovy attacks; this percentage increased to 50% in 4.5 mm larvae and 75% at metamorphosis. Avoidance success from juvenile white seabass attacks ranged from 39% for 3.1 mm larvae to 75% for 7.0 mm individuals and improved to nearly 90% in early juveniles.

Statistical comparison of the responses and escapes from northern anchovy versus white seabass predators indicated that a significantly higher percentage of larvae >6.0 mm SL

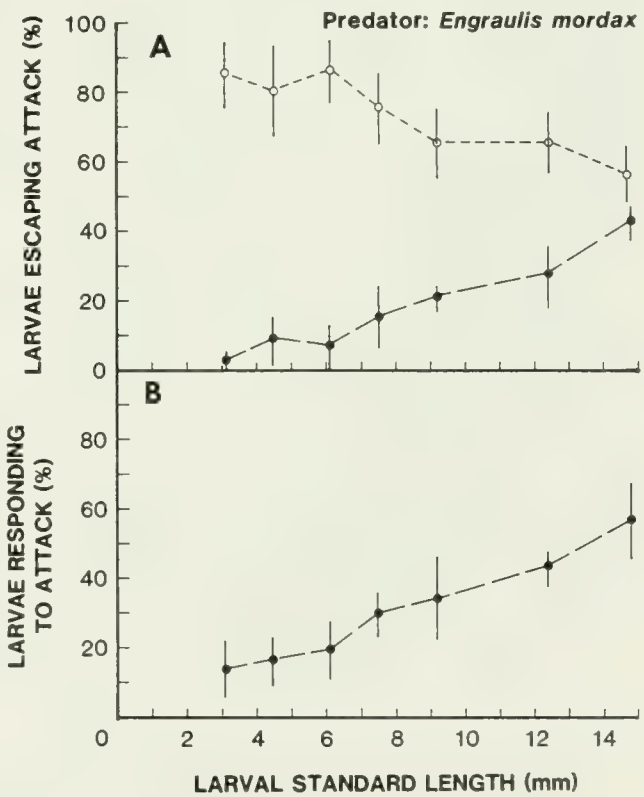

FIGURE 2.—Vulnerability of white seabass larvae to adult northern anchovy predators as a function of larval length. A. Solid circles are percentage of larvae escaping an attack, error bars are 2 × SE, regression equation is Arcsine $Y = 5.078\ e^{0.144SL}$ ($n = 44$, $r^2 = 0.73$), where Y = proportion of larvae escaping and SL = larval standard length (mm); open circles are percentage of larvae eaten in 10 min trials, error bars are 2 × SE, regression equation is Arcsine $Y = 81.326\ e^{-0.035SL}$ ($n = 44$, $r^2 = 0.96$), where Y = proportion of larvae eaten in 10 minutes and SL = larval standard length (mm). B. Percentage of larvae responding to an attack, error bars are 2 × SE, regression equation is Arcsine $Y = 15.293\ e^{0.081SL}$ ($n = 44$, $r^2 = 0.89$), where Y = proportion of larvae responding and SL = larval standard length (mm).

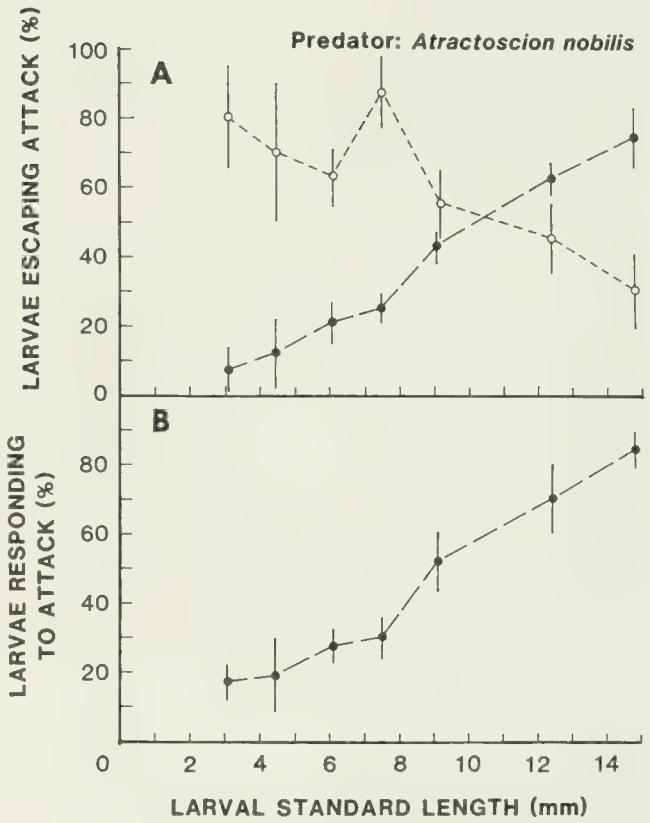

FIGURE 3.—Vulnerability of white seabass larvae to juvenile white seabass predators as a function of larval length. A. Solid circles are percentage of larvae escaping an attack, error bars are 2 × SE, regression equation is Arcsine $Y = 10.976\ e^{0.120SL}$ ($n = 44$, $r^2 = 0.89$), where Y = proportion of larvae escaping and SL = larval standard length (mm); open circles are percentage of larvae eaten in 10 min trials, error bars are 2 × SE, regression equation is Arcsine $Y = 81.210\ e^{-0.048SL}$ ($n = 44$, $r^2 = 0.92$), where Y = proportion of larvae eaten in 10 minutes and SL = larval standard length (mm). B. Percentage of larvae responding to an attack, error bars are 2 × SE, regression equation is Arcsine $Y = 16.822\ e^{0.095SL}$ ($n = 44$, $r^2 = 0.94$), where Y = proportion of larvae responding and SL = larval standard length (mm).

TABLE 3.—Avoidance success of responding larvae (numbers escaping/numbers responding).

	Predator type			
	Northern anchovy		White seabass	
Larval SL (mm)	$\bar{x}$ escape success	SE	$\bar{x}$ escape success	SE
3.2	21.4	4.9	38.8	7.1
4.3	47.0	11.5	57.9	9.1
6.8	63.0	13.2	70.0	7.0
7.4	51.7	6.7	80.0	7.5
9.2	58.8	7.3	81.1	6.6
12.4	64.3	5.3	90.0	5.1
14.8	75.0	6.0	88.0	4.5

escaped white seabass attacks, while a significantly higher percentage of larvae >7.5 mm SL responded to white seabass attacks (ANCOVA with Least Squares Means, $P < 0.05$). This increased responsiveness to white seabass predators (compared to northern anchovy) translated into significantly reduced consumption rates by white seabass predators on larvae >8.5 mm SL (ANCOVA with Least Squares Means, $P < 0.05$).

Larval Visual Ontogeny

The Retina and Visual Acuity

Histological examination of the white seabass visual system revealed numerous developmental changes from hatch to juvenile metamorphosis. In yolk-sac larvae, the lens was present, but the retina was unpigmented and undifferentiated. At time of yolk absorption (ca. 3.2 mm SL), the retina became differentiated into distinct layers, the photoreceptive layer contained visual cells and the epithelial (basal) layer became pigmented. Presumably, at this stage the eye was functional.

In young larvae (3.5–7.0 mm SL), the retina appeared to be composed of only cone cells and no retinomotor (light-dark) responses were noted by either the photoreceptor cells or the epithelial masking pigment. In larvae >4 mm SL, the posteroventral area of the retina (~15–20° below the horizontal plane) was characterized by densely packed cone cells, constituting an *area temporalis*. A lens retractor muscle first appeared histologically at a standard length of 4.5 mm (Fig. 4). Seen in sagittal section, the lens retractor articulated posteriad with the ventral

floor of the retina and anteriad to the lens by means of an extremely thin ligament. In older larvae and juveniles, the lens retractor became bipartite, presumably aiding in movements of the lens posteriad and/or ventrad.

The outer nuclear layer (ONL) of the retina, containing the photoreceptive cell nucleii, was single-tiered until larvae reached a length of 7.0–7.5 mm SL. At this stage, compact and darkly staining mitotic bodies began to appear in the ONL (Figs. 5, 6A); these mitotic bodies appeared to be rod precursors. At a larval length of 10.5 mm SL, double cones were present in the photoreceptive layer and the ONL was multitiered. At 12.5 mm SL the ONL nucleii were multilayered and a clear retinomotor response was evident, indicating the presence of rods (Figs. 6A, 7).

During ontogeny the density of cone cells in the photoreceptive layer decreased linearly, while lens diameter increased linearly (Fig. 6B). Visual acuity improved nonlinearly with larval size, changing from 91 minutes of arc in first-feeding larvae to 26 minutes in metamorphosing fishes (Fig. 6A). The period of most rapid improvement in acuity occurred from approximately 4–9 mm larval length.

Development of the Optic Tectum

In yolk-sac larvae, the optic tectum of the mesencephalon (midbrain) was composed of undifferentiated matrix cells. During early feeding stages, the tectum differentiated into an inner, neuronal *stratum periventriculare* (SPV) and an outer, fibrous *stratum zonale* (SZ) (Fig. 8). This bilayered configuration persisted throughout the larval stages, with the entire tectum and the outer SZ thickening during ontogeny (Fig. 9A, B). The period of most rapid tectal differentiation during the early life stages occurred from approximately 3 to 9 mm larval

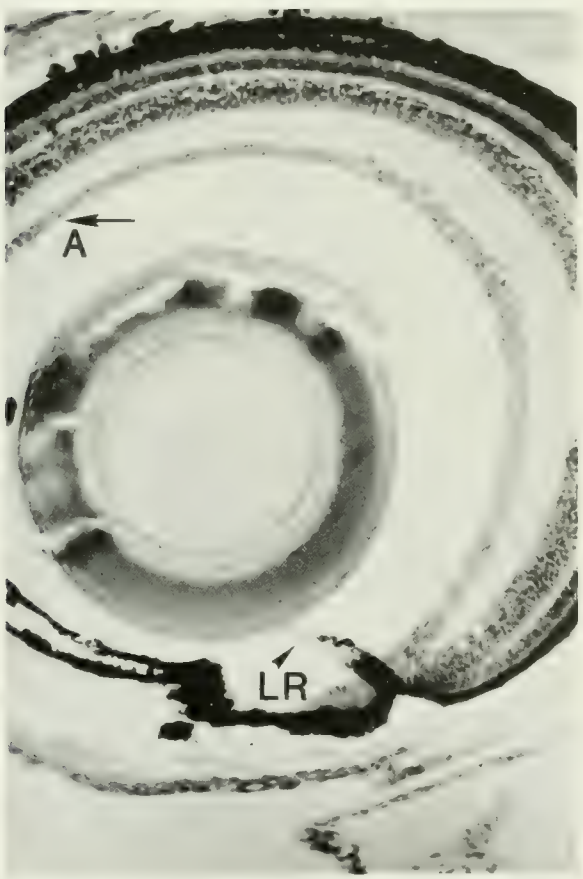

FIGURE 4.—Sagittal section of the eye of a 4.8 mm SL white seabass larva showing the position of the lens retractor muscle (LR). (A) indicates the anterior direction. ×100.

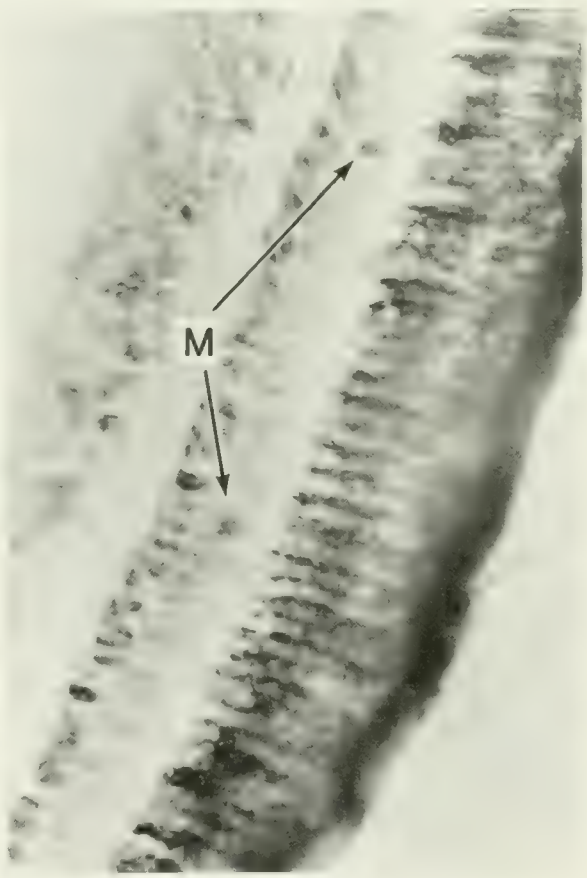

FIGURE 5.—Cross-section of the retina of an 8.0 mm SL white seabass larva showing several dark mitotic bodies (M) in the outer nuclear layer. ×250.

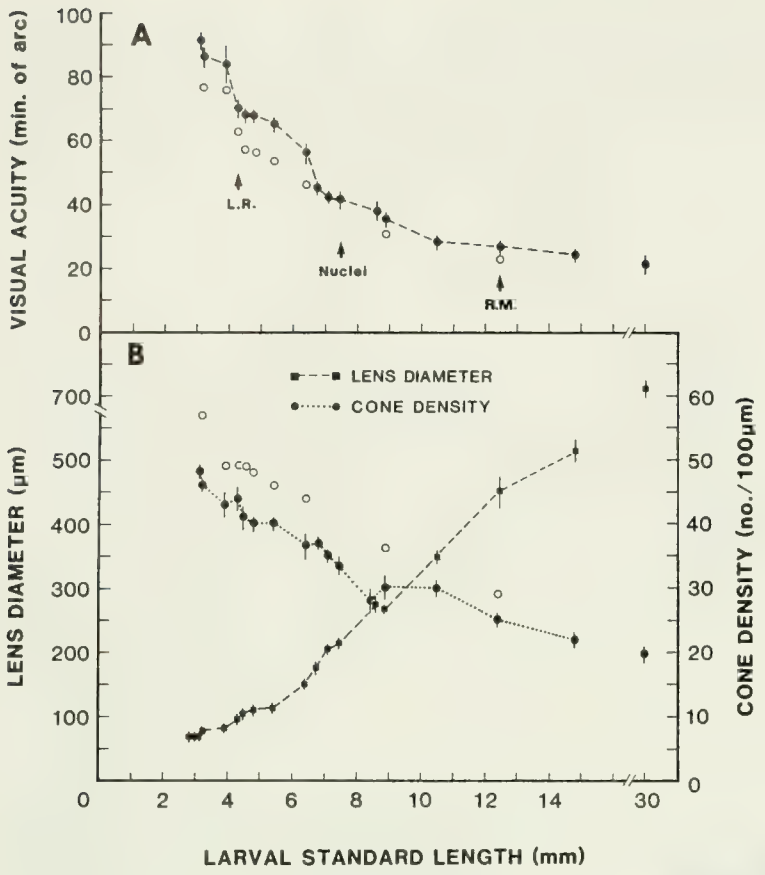

FIGURE 6.—Visual development of larval white seabass as a function of larval length. A. Visual acuity, error bars are 2 × SE, regression equation is $Y = 138 - 18.2\,SL + 0.726\,SL^2$ ($n = 66$, $r^2 = 0.96$), where Y = visual acuity (min of arc) and SL = larval standard length (mm). L.R. is the first appearance of the lens retractor muscle; Nuclei is the first appearance of mitotic bodies in the outer nuclear layer; and R.M. is retinomotor response. B. Squares are changes in lens diameter, error bars are 2 × SE, regression equation is $Y = -58.7 + 37.8\,SL$ ($n = 78$, $r^2 = 0.97$), where Y = lens diameter (μm) and SL = larval standard length (mm); circles are changes in cone cell density, error bars are 2 × SE, regression equation is $Y = 52.6 - 2.3\,SL$ ($n = 66$, $r^2 = 0.89$), where Y = cone cell density (no./100 μm) and SL = larval standard length (mm). Open circles are measurements taken in the *area temporalis*. Values for a 30 mm SL juvenile are given for comparison to larvae.

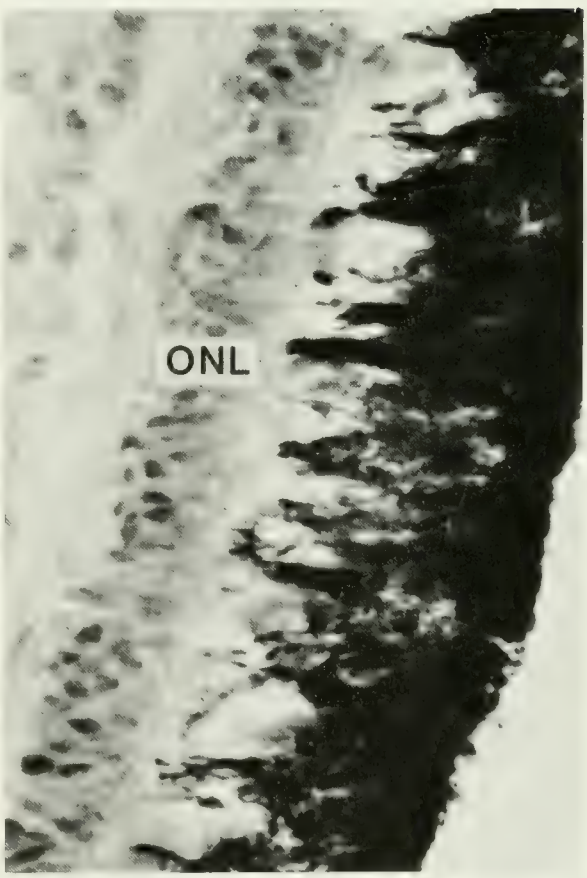

FIGURE 7.—Retinomotor response of a 12.5 mm SL, light-adapted white seabass larva, showing migration of the epithelial masking pigment. ONL is the outer nuclear layer. ×400.

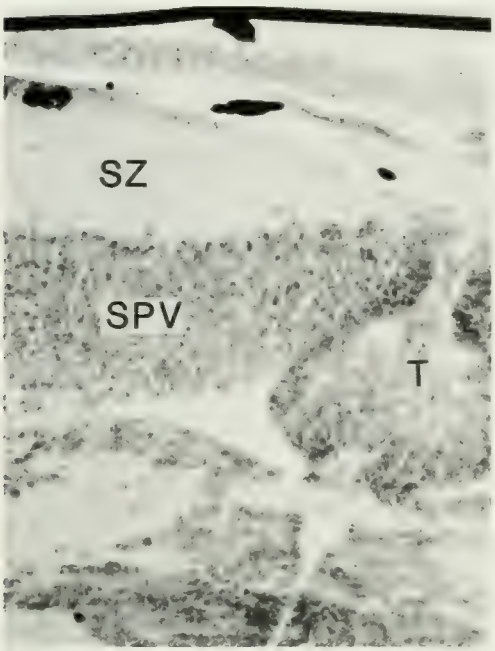

FIGURE 8.—Cross-section through the optic tectum of a 9.2 mm SL white seabass larva. The tectum is bilayered at this stage, with an inner *stratum periventriculare* (SPV) and an outer *stratum zonale* (SZ). The SZ is thickening and exhibits increasing numbers of neurons migrating from the inner layer. The *torus longitudinalis* (T) is quite prominent by this stage. ×100.

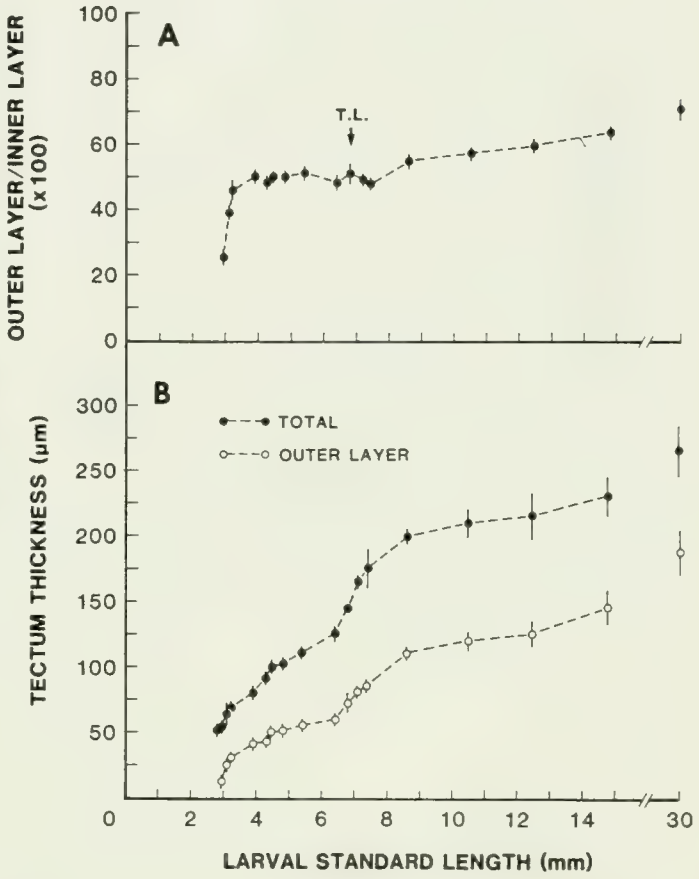

FIGURE 9.—Development of the optic tectum of larval white seabass as a function of larval length. A. Change in the ratio of the outer layer/inner layer, T.L. is the first appearance of the *torus longitudinalis*. B. Solid circles represent total thickness of tectum, error bars are 2 × SE, regression equation is $Y = -48.6 + 38.8\ SL - 1.35\ SL^2$ ($n = 64$, $r^2 = 0.97$), where Y = total width of tectum (μm) and SL = larval standard length (mm); open circles represent thickness of outer layer, error bars are 2 × SE, regression equation is $Y = -33.8 + 20.3\ SL - 0.56\ SL^2$ ($n = 60$, $r^2 = 0.97$), where Y = width of outer layer (μm) and SL = larval standard length (mm). Values for a 30 mm SL juvenile are given for comparison to larvae.

length (Fig. 9B). Growth and differentiation of the SZ appeared to involve cell migrations from the inner SPV with a progressive increase in the SZ:SPV ratio (Fig. 9A). This ratio increased rapidly at first feeding (~3–4 mm SL), stayed constant at lengths of 4.0–7.5 mm SL, and then increased again from 7.5 mm to early juvenile stages.

Another important event in the ontogeny of the optic tectum involved the development of the *torus longitudinalis* (TL). This structure first appeared histologically at a larval length of 6.8–7.0 mm SL (Fig. 9A). Seen in transverse section, the TL developed as a teardrop-shaped structure with a wide area of contact dorsad with the optic tectum and ventrad with the epithalamus (Fig. 8). The TL continued to grow with ontogeny, and in older larvae and early juveniles the TL exhibited an increasing number of neuronal projections to the cerebellum.

Ontogeny of Mechanoreceptors

Neuromast Development

Staining with Janus Green provided somewhat variable results, in that not all white seabass larvae took up the stain equally well. Some neuromast organs stained better than others, but the use of 6–8 fish per larval size class seemed to provide good composite patterns of neuromast formation.

At hatching, larvae had 5 or 6 pairs of neuromasts on the head and 5 or 6 pairs extending along the trunk (Fig. 10A, B). All of these organs appeared to be free neuromasts (not enclosed by canals). Each free neuromast consisted of a basal, naked neuromast organ attached apically to a cylindrical, gelatinous cupula. The only other stained structures were the nasal pits.

The total number and patterned formations of free neuromasts increased with ontogenetic development (Figs. 10, 11). At first feeding, larvae had 6–8 neuromasts on the head and 6 or 7 on the trunk. During development, new head neuromasts appeared first in the supraorbital and infraorbital areas, while on the trunk they recruited midlaterally (Fig. 11). The period of most rapid addition of free neuromasts was in the larval size range of 4–9 mm SL. During the early postflexion stage (~7–10 mm SL), free neuromasts began to form in distinct supraorbital, infraorbital, and preopercular (hyomandibular) rows on the head and in a single midlateral row on the trunk (Figs. 10, 11). By 12.5 mm SL,

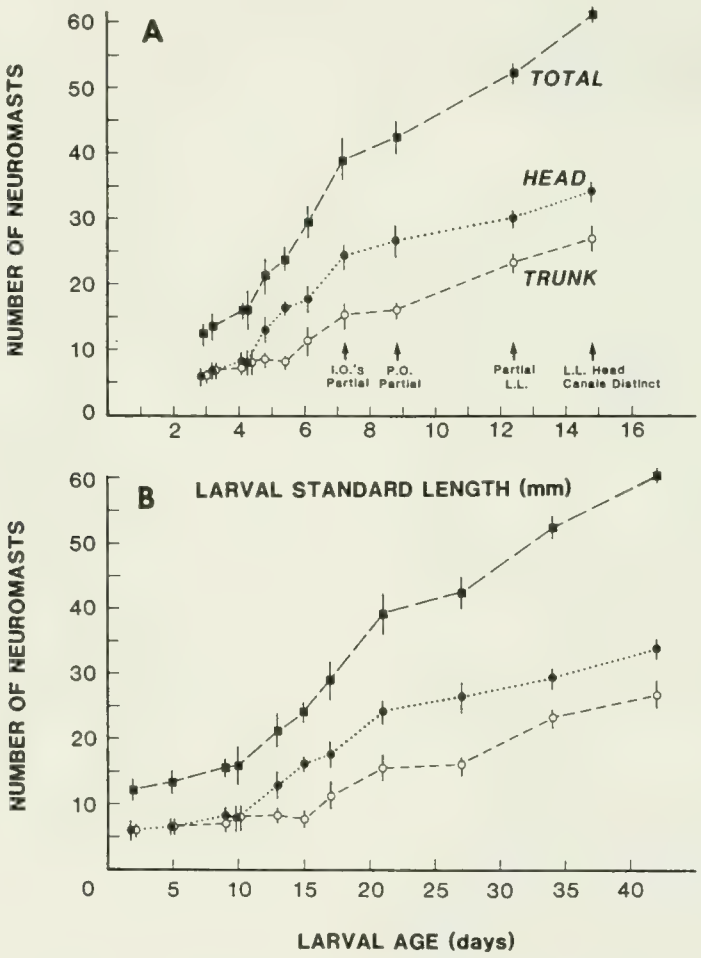

FIGURE 10.—Numbers of free neuromasts developing on larval white seabass as a function of larval length (A) and age (B). Error bars are 2 × SE. I.O.'s are infraorbital and supraorbital rows on the head; P.O. is the preopercular or hyomandibular row on the head; and L.L. is the lateral line. Values are based on staining and should be considered approximate only.

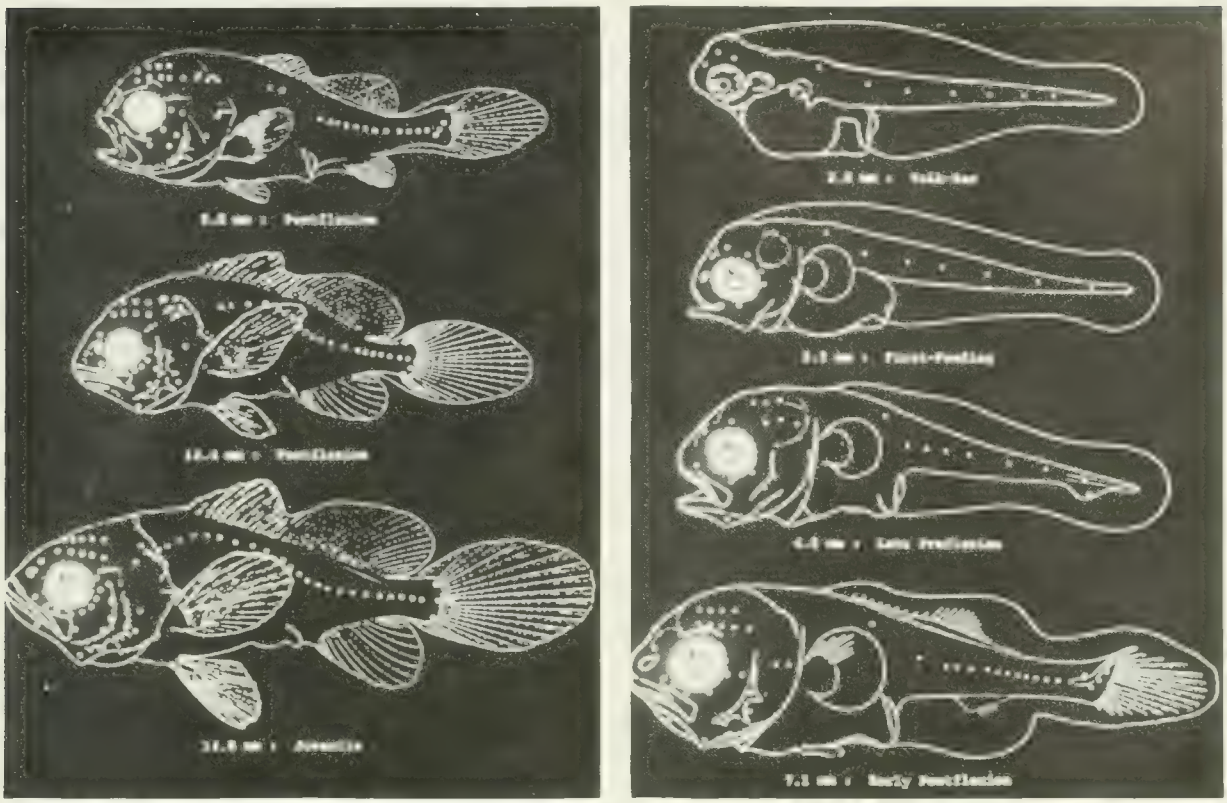

FIGURE 11.—Composite maps showing the location of free neuromast organs during development of white seabass larvae. Larval outlines were modified from those of Moser et al. (1983).

some of the recruiting neuromasts were being enclosed by canals on the head and trunk; some existing free neuromasts were being incorporated in canals as well. At juvenile metamorphosis, the three major branches of the head canals, as well as the lateral line on the trunk, were fairly distinct (Figs. 10A, 11), forming the precursor to the juvenile and adult lateral line system.

Swimbladder Development

In yolk-sac larvae, the swimbladder appeared as a collapsed sac dorsad to the yolk sac, while in first-feeding larvae it was still partially flattened and situated dorsad to the anterior digestive tract. Timing of complete swimbladder inflation was variable; most larvae exhibited full inflation at lengths of 4.5–5.5 mm SL. In larvae >4 mm, a pneumatic duct was present in the anterodorsal area of the swimbladder. It was not clear whether swimbladder inflation occurred by way of air-gulping at the surface or by gas secretion internally.

DISCUSSION

Neurosensory Basis For Avoidance Responses

The overall probability of white seabass larvae escaping predatory attacks seems highly dependent on the size of the larvae, the type and quality of sensory input being integrated by the larvae, and the type of predator encountered (Fig. 12). Yolk-sac larvae have nonfunctional eyes, a small number of free neuromast organs on the head and trunk, and a noninflated swimbladder. At first feeding (~3.2 mm SL), the eye becomes functional, but visual acuity is poor; the pure-cone retina limits peripheral vision and motion detection, and no accommodation is possible (since there is no lens retractor muscle). There is strong correlative evidence that increases in numbers of free neuromasts and improvements in the visual system are responsible for the improved avoidance responses observed in predation trials. In larvae <4.5 mm SL, predator detection is most likely a function of mechanoreception by free neuromasts, since visual

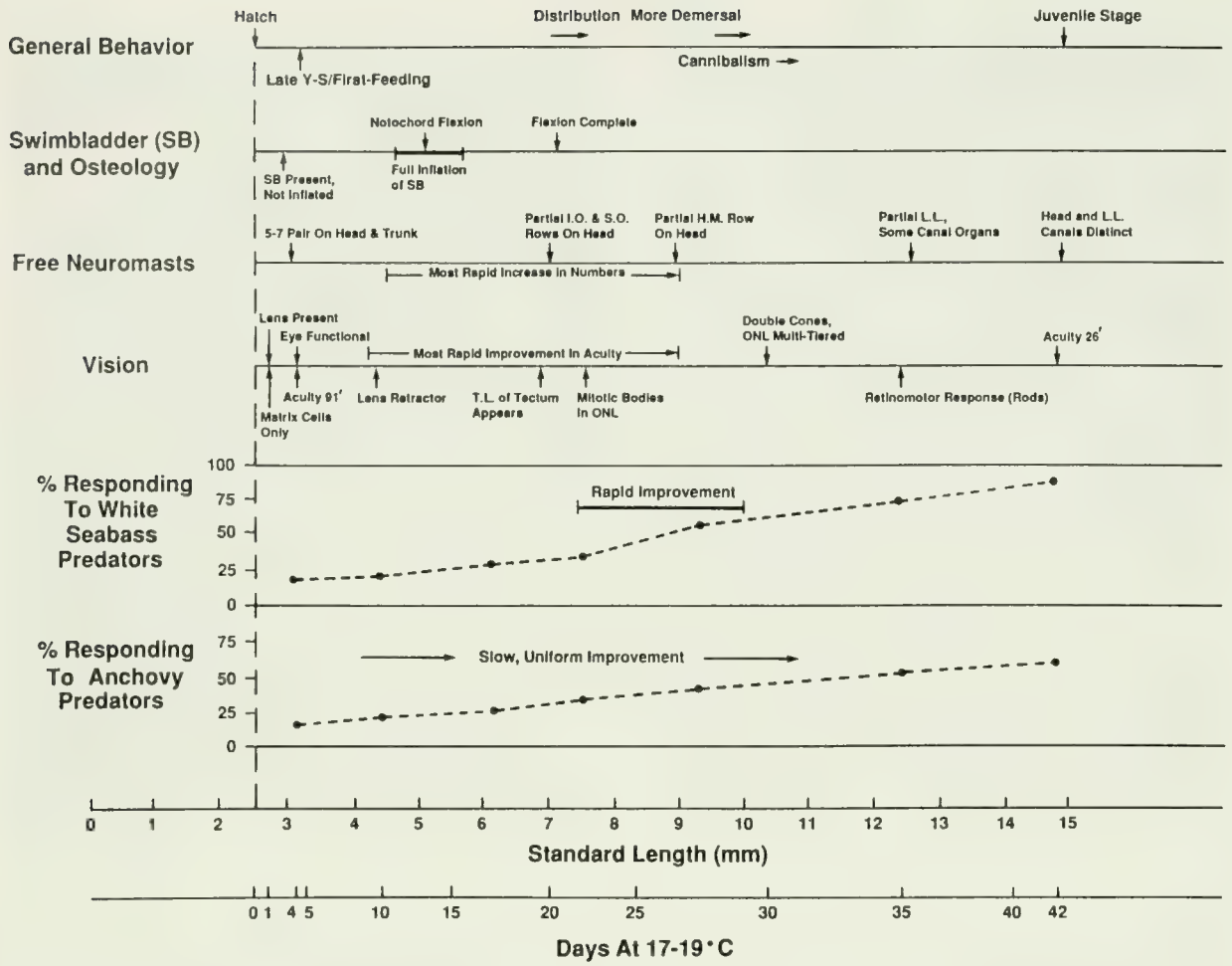

FIGURE 12.—Developmental events and sensory system development during the early life history of the white seabass. Format is based on Hunter and Coyne (1982). Developmental data are from my study, except some behavioral data from Orhun (unpubl. data) and osteological data from Moser et al. (1983). Y-S = yolk-sac stage, I.O. = infraorbital, S.O. = supraorbital, H.M. = hyomandibular, L.L. = lateral line, T.L. = *torus longitudinalis*, ONL = outer nuclear layer of retina.

acuity is poor and no acoustic inputs are likely through the swimbladder. During notochord flexion (~5–7 mm SL), visual accommodation is developed with the lens retractor muscle, the swimbladder is inflated (potentially providing acoustic stimuli), and there begins a major recruitment of free neuromasts on the head and trunk. Up to this point in development, it would appear that vision plays a limited role in predator detection.

During the early postflexion stage (~7 mm), the visual system begins to undergo numerous changes (Fig. 12). Acuity continues to improve, early rod precursors develop in the retina, the optic tectum increases markedly in size and stratification, and the *torus longitudinalis* begins to develop in the midbrain. At 10.5–12.5 mm SL, double cones and early rod cells are present in the retina. These changes are essential to visual improvement and integration. Visual acuity calculated for most adult marine fishes is 2–10 minutes of arc (Tamura 1957); values for adult white seabass are unknown but probably fall in this range. Thus, approximately 75–80% of the improvement in acuity seen from hatch to adult stage in white seabass has occurred by the late larval stage. However, for vision to play a major role in predator detection, improvement in acuity must be accompanied by development of rod cells, by accommodation to distant objects (lens retractor muscle), and by growth and development of the optic tectum. The development of rod vision helps to improve peripheral vision (O'Connell 1981) and motion detection (Blaxter 1986), both crucial aspects of predator detection. Rods also aid in improved visual performance in dimmer light (O'Connell 1981), which would improve foraging skills and predator-detection

as white seabass become more demersal. Growth and stratification of the optic tectum allow for more complex interconnections with other brain centers in teleosts and are essential for the development of progressively more sophisticated behavioral responses (Munro 1984). The *torus longitudinalis* functions in midbrain integration of proprioceptive information (Groman 1982) and is involved in the control of visual motor patterns (Munro 1984).

The free neuromasts in fish larvae probably function in detection of differences in velocity between the fish and surrounding water. The incorporation of neuromasts into canals (as occurs in older white seabass larvae and early juveniles) probably aids in schooling or detection of accelerations in water movements caused by other animals, such as predators (Blaxter et al. 1983). The increases in numbers and in patterned formations of neuromasts with white seabass larval size probably improve detection of predator movements and aid in swimming movements and proprioception.

During the early postflexion stage (7.5–10.0 mm SL), these improvements in mechanoreceptive and visual capabilities appear to be directly related to improved detection and escape responses. However, depending upon the type of predator encountered, a significant difference exists in the degree of improvement in avoidance capabilities (Fig. 12). Early postflexion larvae exhibit a modest improvement in evading northern anchovy attacks, but display a dramatic improvement in detecting and escaping the slower, more discontinuous attacks of juvenile white seabass. Since some startle responses are elicited even in yolk-sac larvae, it appears that neural motor pathways such as Mauthner-type neurons (Eaton and DiDomenico 1986) are present and functioning during all developmental stages. Just prior to and during the early postflexion stage, larvae undergo notable additions of neuromast organs and major improvements in the visual system. Since the outcome of a predator-prey interaction is heavily dependent upon reaction velocity and timing (Webb 1976), the slower, close-range attacks of juvenile white seabass probably allow more time for detection of sensory stimuli from several modalities as well as sensory-motor integration needed for response and escape movements.

Improvements in visual and mechanoreceptive systems have been implicated in the evasion behaviors of northern anchovy larvae (Webb 1981; Folkvord and Hunter 1986), while acoustic stimuli detected through the gas-filled otic bullae seem important in the development of startle responses of Atlantic herring larvae (Fuiman 1989). The inflation of the otic bullae with gas and the occurrence of a well-developed acousticolateralis system, however, seems to be more characteristic of clupeoid larvae (Fuiman 1989). Although acoustic stimuli or Rohon-Beard (mechanoreceptive) input could also be related to improved evasion responses of white seabass larvae, the observed improvements in the neuromast and visual systems seem to be directly related to the improved avoidance capabilities.

Larval Vulnerability to Attacks

Larval size and developmental stage are the most important factors related to larval vulnerability in laboratory trials. The type of predator encountered also influences predation rates. However, although white seabass larvae were better able to respond to juvenile white seabass attacks than those of northern anchovy, this did not result in significantly reduced predation rates (in comparisons between predator types) until larvae were >8.5 mm in length. This suggests that other factors related to predator detection of prey, such as prey morphology, water clarity, and alternative prey abundance, may be as important as predator type in controlling vulnerability of small white seabass larvae. Physical background and morphological conspicuousness of prey can be important factors controlling predation rates of planktivorous fishes (Vinyard and O'Brien 1976), while relative abundance of alternative prey has been shown to have significant effects on fish consumption rates on small white perch larvae (Margulies in press).

One disadvantage of laboratory studies is that realistic encounter rates between larval prey and fish predators are difficult to simulate. Although the main purpose of this study was to delineate the developmental basis for larval avoidance behaviors, it is important to recognize the limitation of predicting total vulnerability of larvae based on laboratory trials only. Total vulnerability to predation is a function of the probability of encounters between predator and prey, the probability of capture of prey and the probability of attacks by a predator (O'Brien 1979). My data provide reliable estimates of probability of prey capture and, to a lesser degree, probability of attacks by the experimental fish predators. Encounter rates, however, are affected by a

number of larval growth-related parameters, including increased larval swimming speeds and search volumes and increased conspicuousness of larger larvae (Hunter 1981). It is possible that increasing encounter rates between a suite of predators and larger white seabass larvae in natural systems would offset the observed steady increase in detection and escape responses observed in larger larvae in laboratory trials. This could occur until larvae became invulnerable to attacks. My laboratory data provide some hint of this pattern in the slightly increased predation rates on larvae in the 4.5–7.5 mm size range (see Figures 2A, 3A). However, white seabass larvae are relatively inactive and become increasingly demersal during ontogeny, thus, they might not be subject to significantly higher encounter rates with predators. This remains speculative, however, and is an area for future investigation.

Implications for White Seabass Early Life History

Compared with white seabass larvae, California sardine, *Sardinops sagax*, and northern anchovy larvae (co-occurring pelagic larvae in nearshore southern California waters) appear better able to detect and avoid attacks by adult northern anchovy predators at comparable stages of larval development (Folkvord and Hunter 1986; Butler and Pickett 1988). These two clupeoid species also exhibit schooling behavior in the later larval stages. Many species exhibit a combination of larval adaptations to minimize fish predation, including long periods of transparency (e.g., dover sole, *Microstomus pacificus*; Hunter[1]), rapid development of avoidance capabilities (northern anchovy and sardine) and schooling (clupeoids). During early feeding stages, white seabass larvae develop a robust, highly pigmented body form and exhibit limited mobility. During the early postflexion stage (7–10 mm), white seabass start to abandon a strictly pelagic distribution and become noticeably more demersal. By the late larval and early juvenile stage, they are found almost exclusively associated with submerged cover (often drift algae) or near-bottom habitats (pers. obs.; Allen and Franklin 1988; Orhun[2]; Kramer[3]). In nearshore waters of southern California, other sciaenid larvae show a marked vertical size distribution during daylight hours, with larger larvae (postflexion and larger) occurring in highest densities in suprabenthic habitats and smaller larvae occurring higher in the water column (Love et al. 1984; Jahn and Lavenberg 1986). The suprabenthic distribution of larger larvae has been characterized as a possible adaptation to high concentrations of food, for predator-avoidance or for maintenance of position on the continental shelf. However, recent studies of white croaker, *Genyomenus lineatus*, larvae indicate that the suprabenthic distribution of older sciaenid larvae is probably not related to feeding (Jahn et al. 1988).

My results indicate that this ontogenetic shift deeper into the water column by older white seabass larvae (and other sciaenids) may be related to their predator-avoidance capabilities. The dominant planktivorous species encountered in midwater habitats of nearshore southern California waters are fast-swimming, shoaling pelagics such as northern anchovy, sardine, and Pacific mackerel, *Scomber japonicus*. Potential planktivores in near-bottom habitats include sciaenids, gobiids, embiotocids, clinids, serranids, and various flatfishes (Eschmeyer et al. 1983). All of these demersal species exhibit some type of ambush, hovering, discontinuous, or close-range mode of predatory behavior, similar to the attack behavior of juvenile white seabass, and all attack at slower speeds than the shoaling pelagics. Based on my experimental evidence, it is likely that, as they drop out of the plankton, older white seabass larvae maximize their predator-detection and avoidance capabilities when encountering demersal predators. Remaining in the plankton in later larval stages and being exposed to pelagic, shoaling fish predators would prolong a period of extreme vulnerability, while shifting to a demersal distribution would place white seabass in habitats to which they are better suited developmentally.

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[2]R. Orhun. Unpubl. data. Hubbs Marine Research Center, Sea World, San Diego, CA 92109.

[3]S. Kramer. Unpubl. data. Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

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Residence Times, Distribution, and Production of Juvenile Chum Salmon, *Oncorhynchus keta*, in Netarts Bay, Oregon

William G. Pearcy, Christopher D. Wilson, Alton W. Chung, and John W. Chapman

ABSTRACT: Juvenile chum salmon resided in Netarts Bay, a small, shallow estuary at the southern spawning range of chum salmon in the Northeast Pacific, from mid-March until June during each of three years from 1984 to 1986. Early in the spring they were most abundant in beach seine catches during high tide in the upper bay, indicating extensive intertidal excursions. Later in the spring, when temperatures exceeded 14°–16°C in the upper bay, they were most common in catches at low tide in the lower bay. Based on recaptures of fin-clipped hatchery fish, the residence of juveniles varied inversely with size of fish at release. Large (6.5 g) fish immediately emigrated from the estuary and 3–4 times as many returned as adult fish as 1.0 and 2.2 g juveniles, which had residence half-lives of 5–16 days. Growth rates of juvenile chum salmon during the 3 years were similar, but were low (1.6–2.3% body weight/day) compared with other studies. Production was also low. This may be related to high metabolic costs at above optimal temperatures and the large size of available prey in Netarts Bay.

The period of early marine residence is thought to be a critical stage in the life history of Pacific salmon, affecting the survival of young and the numbers of adults returning in subsequent years (Parker 1968; Peterman 1978; Pearcy 1984). The period of estuarine residence may be especially important for chum salmon, *Oncorhynchus keta*, (Healey 1982a; Simenstad and Wissmar 1984). They enter estuaries at a small size and presumably need to grow rapidly to avoid intense predation after they enter the ocean (Parker 1971; Simenstad and Salo 1980; Healey 1982b; Simenstad and Wissmar 1984). The capacity of an estuary to produce salmon may be limited, however, and the availability of prey resources may affect salmon emigration, growth, ability to avoid predation, and thus survival (Reimers 1973 Bailey et al. 1975; Healey 1979, 1980a; Sibert 1979; Simenstad and Salo 1980).

The hypothesis that the estuarine phase of the early life history of chum salmon is critical needs to be tested (Simenstad and Wissmar 1984; Levings 1984). If this phase is essential, increased releases of hatchery fish from private or public hatcheries may not be beneficial unless release strategies minimize or circumvent density-dependent growth and survival in estuaries, e.g., by modifying size, time, or numbers of fish released. Healey (1979, 1982a) concluded that seaward migration was size dependent, and Ioka (1978, unpubl. data) reported that large (>8 g) juvenile chum salmon were capable of migrating directly into offshore waters. This suggests that estuarine rearing may not be essential for chum salmon released from hatcheries at a large size.

To evaluate the capacity of estuaries to produce chum salmon, we studied their downstream movement, distribution, abundance, residence time, growth, and production in Netarts Bay, OR. Netarts Bay is a small estuary along the northern Oregon coast, near the southern distribution of chum salmon along the coast of the northeastern Pacific Ocean (Henry 1953). Netarts Bay was selected for this study because the Oregon State University chum salmon hatchery (Lannan 1975, 1983) enabled experimental releases of chum salmon at different times and sizes, and because the residence times and growth of chum salmon in a small estuary needed to be compared with the results found in estuaries farther north.

Netarts Bay (Fig. 1), located along the northern Oregon coast, has an area of only 10 km^2 at mean high water (MHW). The bay is strongly influenced by the ocean. Salinities generally approach ocean levels. The intertidal volume is about 75% of the volume at MHW; 12% of the Netarts Bay is subtidal (Glanzman et al. 1971;

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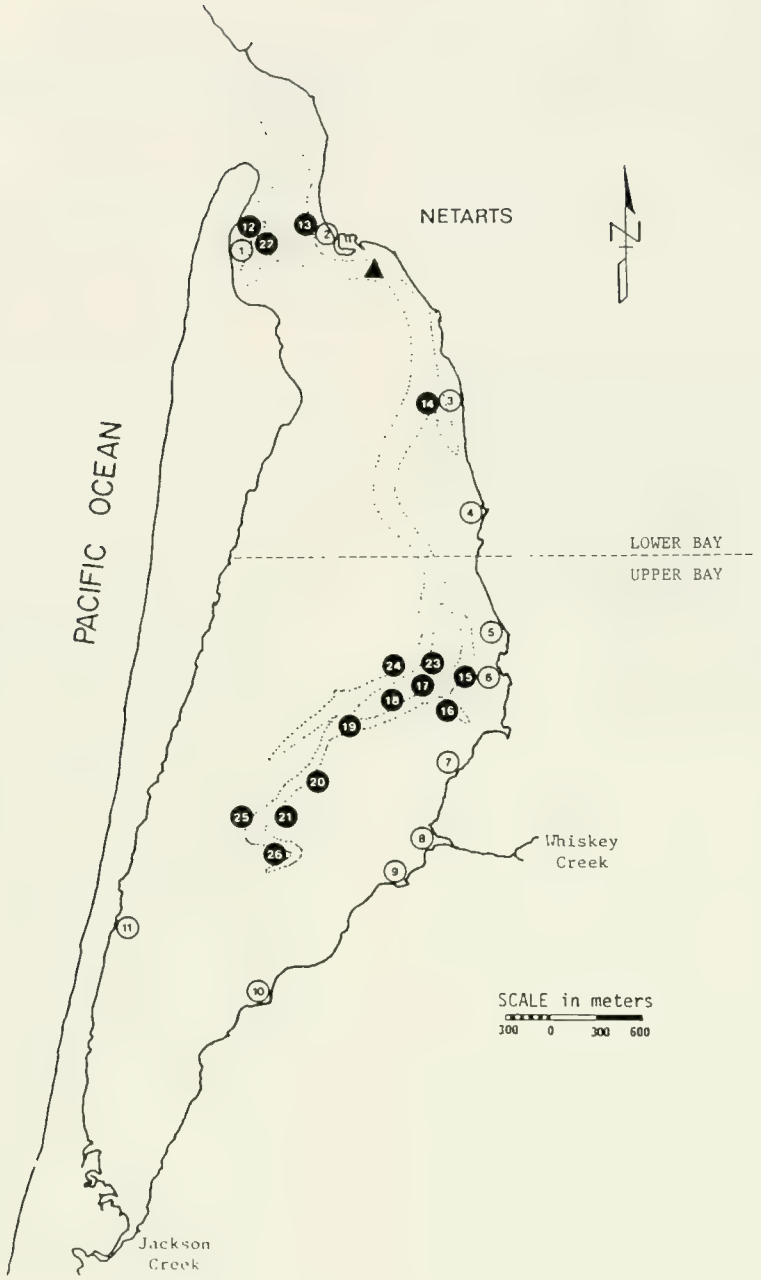

FIGURE 1.—Netarts Bay with locations of high tide (open) and low tide (solid) seine stations and the tow net stations (triangle).

Kreag 1979). The watershed area is small (about 36 km^2), and its only tributaries are small creeks. Whiskey Creek, the site of the Oregon State University experimental hatchery for rearing chum salmon (Lannan 1975), and Jackson Creek are the two largest streams that drain into Netarts Bay and are the major spawning habitats for chum salmon in Netarts Bay. Besides cutthroat trout, only a few rainbow (steelhead) trout and coho salmon were found in Whiskey or Jackson Creek.

METHODS

The contribution of naturally spawned chum fry to Netarts Bay and the timing of their outmigration were estimated from samples of chum salmon fry captured in a fyke net, located in Whiskey Creek about 100 m from the bay at MHW, from late March to early May 1984, and from late February through late May 1985 and 1986. The net, which was used for 35, 51, and 53 days in 1984, 1985, and 1986, respectively, was

constructed of 3.2 mm mesh with a 1.3 m wide mouth opening and two 2.7 m wings. The net was positioned across 95% of the width of the stream except during periods of high stream flow (Wilson and Pearcy 1985a). Catches were monitored during day and night periods. The net was removed from the stream on a few occasions during daylight hours and periods of high stream flow. The sampling error resulting from removing the net during daylight hours is assumed to be minimal as <1% of the total number of chum fry were caught in the fyke net during these hours (Wilson and Pearcy 1985a). Outmigrating juvenile chum salmon were also sampled in Jackson Creek with a 3.2 mm mesh bag net stretched across this stream two nights per week between 19 March and 25 April 1986. Water depth, temperature, cloud cover, and flow rates (1986 only) were recorded from both Whiskey Creek and Jackson Creek during sampling periods. Juvenile chum salmon in the catches were counted and fork lengths (FL) were measured to the nearest 1 mm for all fish or for a subsample of 100 fish per sampling period.

Fin-clipped (ventral and adipose) chum salmon were released from the Whiskey Creek hatchery to estimate residence time and growth of fish entering the bay at different times and different sizes. Data on the releases of marked and unmarked fish are summarized in Table 1. Eggs from adult chum salmon returning to Whiskey Creek were reared at the hatchery and at the Oregon Aqua-Foods, Inc. (OAF) hatchery in Springfield, OR. OAF fish were returned to raceways and acclimated at the Whiskey Creek facility for 10–13 days before release into Netarts Bay. These OAF fish were smaller at release than fish reared at Whiskey Creek in 1984, but were larger than Whiskey Creek fish in 1986 (Table 1). Differential mortality of fin-clipped vs. unclipped fish was not evident for fish held 3–4 days after marking in 1984 and 1985, or for OAF fish marked 10–13 days before release in 1986.

Two problems affected releases of juvenile chum salmon from the Whiskey Creek facility. Some marked fish escaped from the raceway and were caught in the bay before their planned release on 16 April 1984. The second problem was a bacterial disease that afflicted many fish reared at the Whiskey Creek facility in April 1986. About 4.4% of the fish died during marking operations, and 7.7% of the fish that survived marking died after being held in the raceway for 24 hours. Thus the numbers of fish released on 28–29 April 1986 are overestimates of the numbers of healthy fish actually entering the Netarts Bay. The raceway was sterilized with formalin after this release, and no apparent adverse effects were observed on the OAF fish transported to the Whiskey Creek facility in May 1986.

Netarts Bay was sampled for juvenile chum salmon from mid-March through late June 1984 and 1986 and from late February through early

TABLE 1.—Summary of releases of marked and unmarked juvenile chum salmon from the Whiskey Creek hatchery in 1984, 1985, and 1986.

Date	Total no. released × 1000	× FL (mm)	× Wt. (g)	Marks	No. marked × 1,000	% marked
1984						
1 April	215.1–344.1	52	1.4	0		
16 April	516.2–645.2	58	1.9	RV	24.0	
16 April		46	[1]0.75	LV	[2]20.5	
Total	731.3–989.3				44.5	4.5–6.1
1985						
19 April	155.6	56	1.8	RV	18.2	
26 April	218.4	59	1.9	LV	20.2	
Total	374.0				38.4	10.3
1986						
28–29 April	609.0	48	0.97	RV	[3]14.7	
11 May	43.6	62	2.2	RV + A	[2]21.4	
11 May		92	6.5	LV + A	[2]22.2	
Total	652.6				58.3	8.9

[1]Measured on 3 April 1984.
[2]Oregon Aqua-Foods Inc. fish reared offsite.
[3]Estimated no. released after mortality.

July 1985. A 37 m long, tapered, floating beach seine, set in a semicircle from the shoreline from a 4.6 m boat with an 18 hp outboard motor, was used for sampling. Sets encompassed about 100 m^2. The seine had a maximum depth of 2.5 m in the bunt and 0.7 m at the ends of the wings. The wings were made of 2.5 cm (stretch) mesh and the bag was made of 0.64 cm mesh. We sampled 11 high tide stations (1–11) and 10 low tide stations (12–21) in 1984–85 and 11 high tide stations (1–11) and 8 low tide stations (12, 13, 14, 22–26) in 1986 (Fig. 1). (Specific beach seine stations are described by Wilson and Pearcy (1985a) and Chung and Pearcy (1986).) The numbers of beach seine hauls made in 1984, 1985, and 1986 were 435, 333, and 388, respectively. Surface water temperatures were measured to the nearest 0.1°C with a bucket thermometer, and surface salinities were determined to the nearest 2‰ with an American Optical Model 10419[1] refractometer after each set. Each station was sampled several times each month during the field seasons.

We used a Kvichak towed net[2] with a 2.7 × 2.7 m mouth opening and a 8.2 m long body section with mesh grading from 3.8 cm to 0.3 cm and a cod end of 0.3 cm mesh to sample juvenile chum salmon in the main tidal channel during slack tide at approximately 2 wk intervals from late March through late June 1985. One nighttime tow was made. Two boats were used to pull the net along a 900 m long transect in the main channel of the lower bay (Fig. 1) at speeds of about 1–2 m/s.

Approximately 100 individual juvenile chum salmon from each seine haul were checked for fin clips. We assumed negligible regeneration of clipped fins during the 3 mo sampling period. A subsample of 5–50 juvenile chum salmon was preserved in 10% formalin or 95% ethanol for length measurements and stomach content analysis or age determination, respectively. The remaining fish were released. Fork lengths of all preserved fish were measured to the nearest mm. These lengths were converted to fresh fish lengths or weights from the regressions of individual preseved lengths and weights on fresh lengths and weights (Wilson and Pearcy 1985a, b).

For data analysis, the 1984, 1985, and 1986 field seasons were divided into 21, 17, and 18 sampling periods, respectively, in which every beach seine station was usually sampled at least once. Stations were divided into the lower bay (stations 1–4, 12–14, and 22) and upper bay (stations 5–11, 15–21, and 23–26) (Fig. 1). Sand sediments predominate in the lower bay, whereas fine sands and silt, with high organic carbon, are common in the extensive tidal flats of the upper bay (Kreag 1979). Ninety-five percent confidence intervals of the median number of fish caught per set were calculated by the method presented in Snedecor and Cochran (1980). Mean lengths of fish from different regions of the bay were compared using a t-test for unequal variances (Sokal and Rohlf 1981). Growth rates among years were estimated from regressions of the size of recaptured marked fish and compared, using analysis of covariance (Snedecor and Cochran 1980). Growth in weight was calculated from length-weight regressions.

The total numbers of juvenile chum salmon remaining in the bay were estimated by a modified Peterson model (Healey 1980), where on day t,

$$N_t = \frac{CM}{R} \tag{1}$$

where N_t = total population,
C = total catch,
M = estimated number of marked fish present in the bay, and
R = number of marked fish recaptured.

The estimated number of marked fish present, M, was calculated assuming a constant loss rate of marked fish with time:

$$M = M_0\, e^{-kt}$$

where M_0 = total number of marked fish released,
k = instantaneous rate of disappearance of marked fish, and
t = days since release.

The actual number of marked fish recaptured and the estimated number of marked fish from each release group were pooled for each year and used in a modified Peterson model to estimate population numbers (N_t). The instantaneous rate of disappearance of marked fish was estimated for each marked group by the slope of the regression of time on catch per effort. This instan-

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service. NOAA.

[2]Research Nets, Inc., Bothell, WA.

taneous loss rate, k, also provided an estimate of the residence time for each marked group in the estuary. Solving Equation (2) for t when $M/M_0 = ½$ gave the residency half-life in days, the time in which the number of fish had declined by 50%.

The estimated number of fish in the estuary (N_t) was multiplied by the average weight of marked fish to estimate the biomass of juvenile chum salmon present during each sampling period. These biomass estimates were multiplied by the number of days between sampling periods, summed over the entire period that juvenile chum salmon were present, and multiplied by an average instantaneous growth rate in weight of the marked groups to estimate net production for each year.

RESULTS

Emigration from Fresh water

We estimated an outmigration of 11,900, 23,300, and 15,300 chum salmon fry from Whiskey Creek in 1984, 1985, and 1986, respectively. The early portion of the run was not sampled in 1984. These estimates of naturally reared chum salmon fry equalled 1.4%, 6.2%, and 2.3% of the total chum salmon releases from the Whiskey Creek Hatchery in these years (Table 1). The abundances and temporal changes in catches of chum salmon were similar in Jackson and Whiskey Creeks in 1986 (Fig. 2). Since nearly all wild chum salmon spawned in Whiskey Creek or Jackson Creek, we assumed that the production of fry from naturally spawning chum salmon in the tributaries of Netarts Bay was about twice that of Whiskey Creek. The mean length of chum salmon fry caught was 40 mm in each of the three years in Whiskey Creek, and 41.0 mm in 1986 in Jackson Creek. Large fry (>45 mm), which were indicative of rearing in freshwater (Mason 1974), were not caught.

Nearly all wild chum salmon fry outmigrated into Netarts Bay by the end of April in all years (Fig. 2). Peak numbers of fry were caught in Whiskey Creek on 25 March 1984, 25 March 1985, 11 April 1985, and 8 April 1986. Numbers of emigrating fish were poorly associated with any measured physical variable. Peak catches of chum fry were not correlated with stream temperatures (Fig. 2), although the second outmigration pulse in 1985 followed an abrupt increase in water temperature. Increased outmigration activity of fry was not associated with phases of the lunar cycle as has been reported for other salmonid fry (Reimers 1973; Mason 1975). Stream flow estimated from stream heights appeared positively correlated with peak numbers of emigrating fry in 1984 when large numbers of fish were sampled during or immediately after three of four periods of high flow. The first peak of outmigration in 1985 also occurred during high stream flow; however, subsequent peaks in 1985 and 1986 occurred during periods of declining flow.

Distribution-Abundance in Netarts Bay

Chum salmon were present in Netarts Bay for about 2½ months, from mid-March until early June during each year (Fig. 3). The seasonal abundances of juvenile chum salmon in Netarts Bay were correlated with the emigration of wild fish from streams and with releases of fish from the Whiskey Creek Hatchery facility. Although small peaks in beach seine catches during late March 1984 and in early April 1986 coincided with the peak of outmigration of wild fish from Whiskey Creek, most of the naturally reared fry migrated into the bay before the major peaks in beach seine catches (Figs. 2, 3). The largest peaks in beach seine catches occurred within a few days after releases from the Whiskey Creek Hatchery in all years.

Catches of juvenile chum salmon were greater in the upper than the lower bay during March and April in all years. Conversely, catches were generally greater in the lower than the upper bay during May and June (Fig. 4). These trends indicate that juvenile chum salmon preferentially inhabited the upper bay early in the spring and then moved into the lower bay in late spring. Movement into the lower bay late in spring was correlated with the high water temperatures that occurred in the upper bay during May of each year.

Juvenile chum salmon appeared to avoid temperatures exceeding 14°C. Although they occurred at most temperatures observed in the upper bay during March and April, they usually inhabited waters of minimum temperatures during May and June, when average water temperatures exceeded 14°C (Fig. 5, left panel). The occurrence of juvenile chum salmon predominantly in the upper bay in early spring coincided with average upper bay temperatures of <15°C. Movements to the lower bay (Fig. 4) coincided with upper bay temperatures exceeding 16°C (Fig. 5, right panel). The percentages of chum

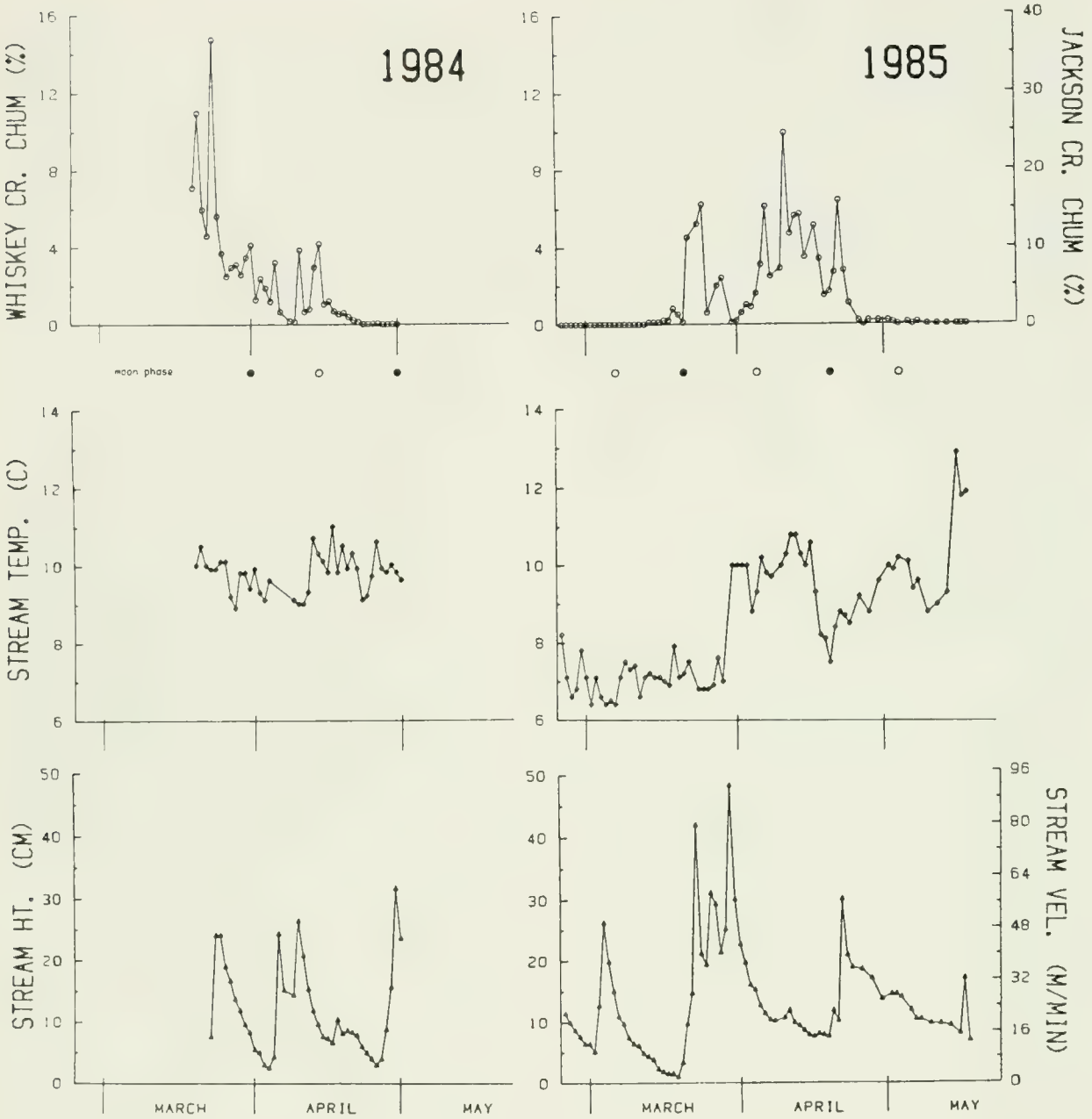

FIGURE 2.—Outmigration of juvenile chum salmon, stream temperatures, and stream height-velocity of Whiskey Creek (1984, 1985, 1986) and Jackson Creek (1986). Solid triangles indicate dates of hatchery releases.

salmon in the upper bay increased only once in all three years when temperatures exceeded 16°C (Fig. 5, 1985).

Schools of chum salmon were sometimes observed in shallow water and variability in the catches of juvenile chum salmon per set was high. The median number of chum caught per set during a sampling date, all stations combined, ranged from 0 to 280. A total of 90 pairs of beach seine sets were made during the three years. The mean (± standard deviation) of the quotient of the largest to smallest numbers of chum caught in the 47 pairs of two sets (each set containing fish) was 5.9 ± 8.8. This indicates that juvenile chum salmon were aggregated in Netarts Bay.

Median catches of juvenile chum salmon during high tide generally exceeded catches at low tide in March and April, and catches at low tide were greater than high tide during May and

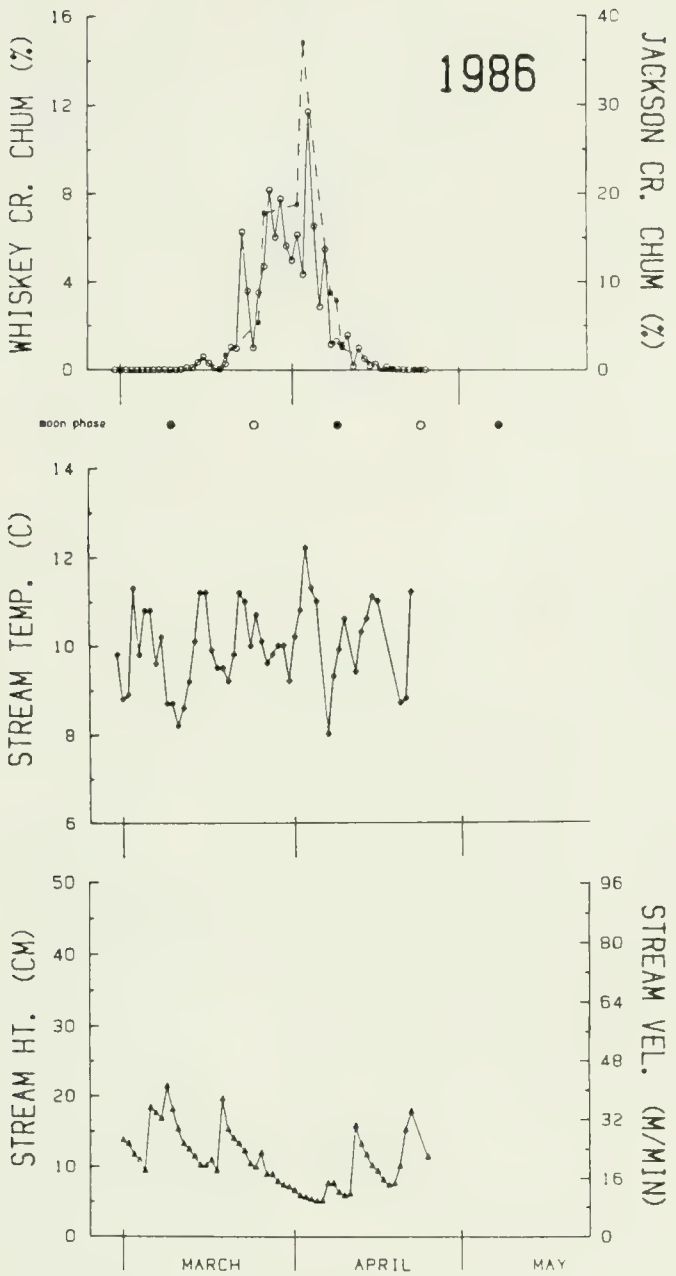

FIGURE 2.—*Continued.*

June of 1984 and 1985 (but not 1986) (Fig. 6). The large catches of juvenile chum salmon along the margins of the bay at high tide, often over 500 m from the low-tide channels in the upper bay, show that they make extensive tidal excursions over the tidal flats during daylight in early spring and actively aggregate along the fringes of the estuary in shallow water.

Juvenile chum were not concentrated in the main channel of lower Netarts Bay between 25 March and 20 June 1985 when tow net hauls were made. Only 38 juvenile chum salmon were caught in the 31 tows (about one fish per 2,000 m^2). Catches in night tows on 22 May were not different from day tows on 21 May (Mann-Whitney U test, $P > 0.1$). Also, the average lengths of chum salmon fish caught in day and night tow net collections and in beach seine collections on 22 May were not significantly different (t-test, $P > 0.1$).

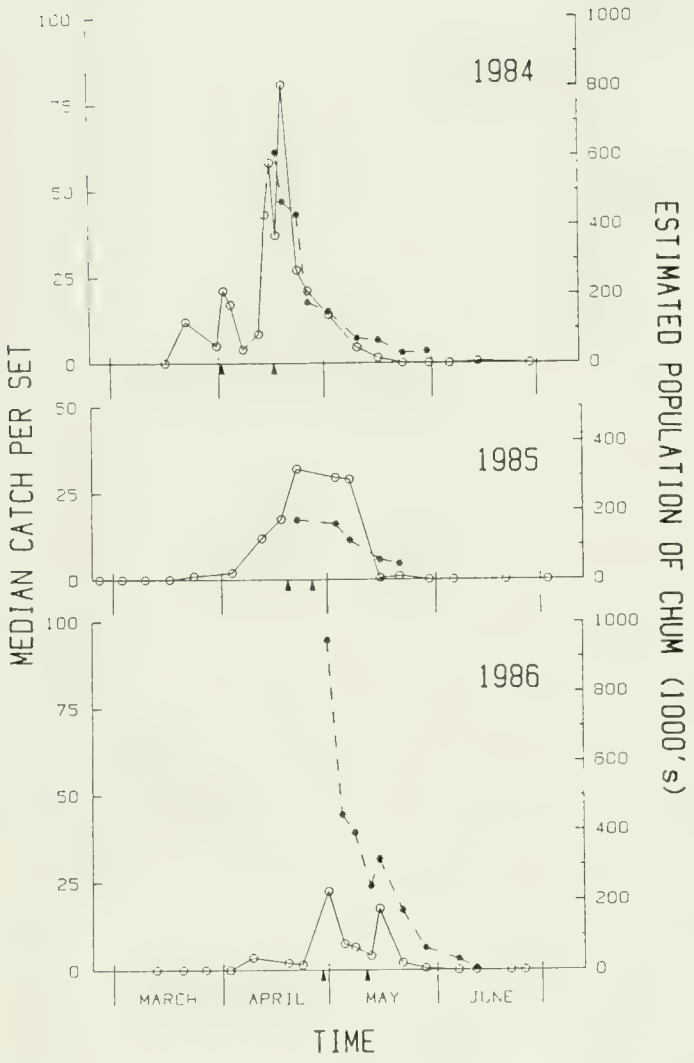

FIGURE 3.—Median catch per beach seine haul of juvenile chum salmon, from all stations combined (solid line) and population estimates based on recaptures of marked fish (dashed line).

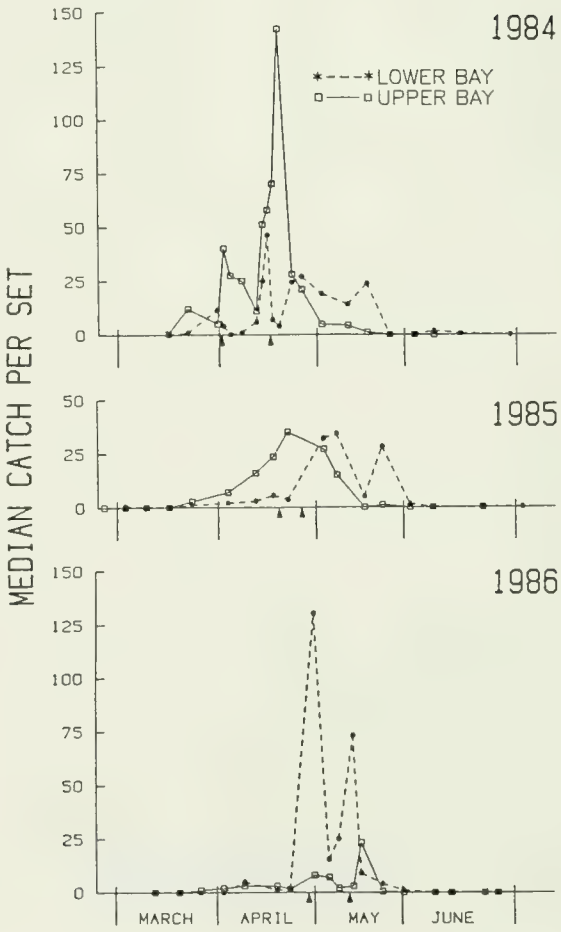

FIGURE 4.—Median catch per seine haul of juvenile chum salmon in the upper (solid line) and lower (dashed line) estuary, and release dates (black triangles).

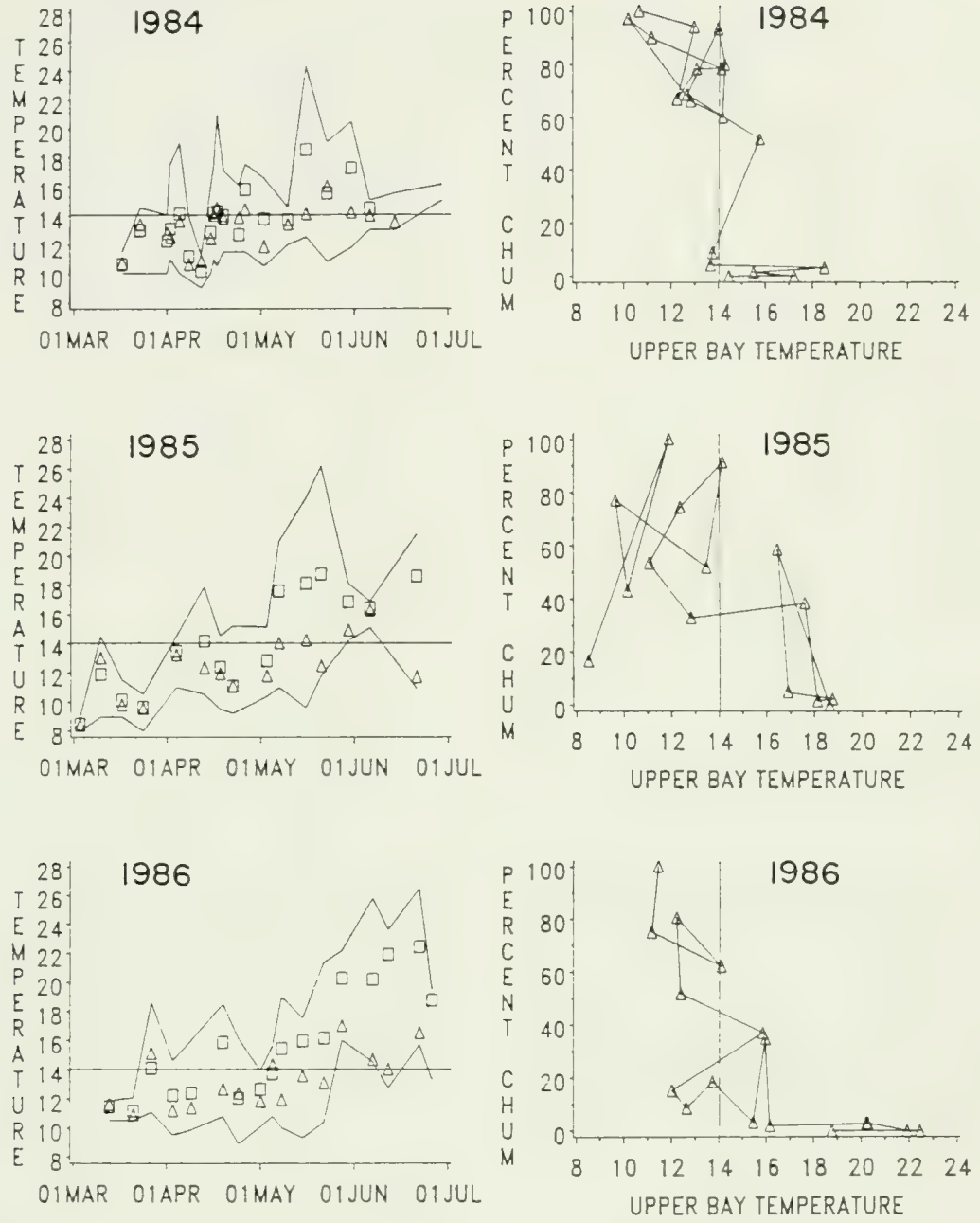

FIGURE 5.—(Left) average temperatures occupied by chum salmon (triangles), average upper bay temperatures (squares) and maximum and minimum temperatures temperatures per collection period (solid lines), and (Right) the percent of juvenile chum salmon collected in upper bay stations vs. average upper bay temperatures (lines connect sequential sampling periods) for 1984, 1985, and 1986. Reference lines indicate 14°C.

Residence Times – Loss Rates

Population estimates based on the total catch showed that the number of marks present, and numbers of marked fish recaptured (Equation (1)), rapidly declined during 1984 and 1986 (Fig. 3 dashed lines; Table 2). The trends shown by mark and recapture estimates and by median seine haul catches were similar in 1984 (Fig. 3). Population estimates on 17 and 18 April 1984 and 3 and 4 May 1985 (1–2 days and 7–8 days after release of all marked fish) were 30% and 57% smaller than the actual numbers of fish released, suggesting rapid decline in numbers soon after release. In 1986, however, the initial population estimate was 55% larger than the number of fish released a week earlier. Marked fish released in April 1986 probably experienced higher mortal-

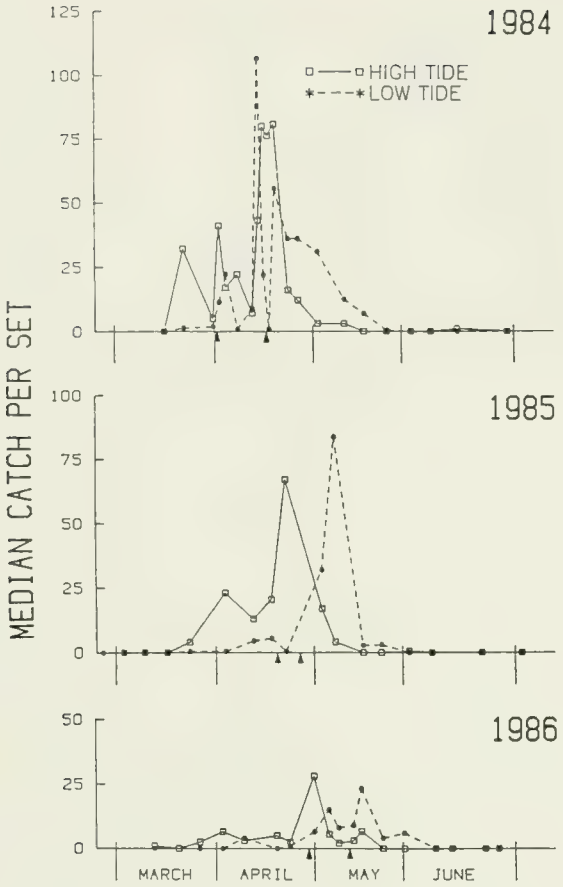

FIGURE 6.—Median catches per seine haul of chum salmon at high tide (solid line) and low tide stations (dashed line), 1984–86. Solid triangles indicate dates of hatchery releases.

ity after release than unmarked fish as a result of the added stress of marking and the debilitating bacterial disease that afflicted this release group. As a result of higher mortality of marked fish, R was low and M was probably overestimated, leading to overestimation of the population (N_t, Equation (1)).

Higher loss rates were found for small than for large fish hatchery chum salmon in Netarts Bay from the decline in the natural logarithm of catch per effort of fin-clipped fish (Table 3). In 1986, the residence half-life (the time for the catch rates to decrease by one-half (Myers and Horton 1982)) was 7.4 days for fish released at 1.0 g, 4.9 days for fish released at 2.2 g and <2 days for fish released at 6.5 g. None of the largest fish was captured 2 days after release or during subsequent sampling. Presumably these large fish emigrated rapidly from the estuary. An anomaly in the trend for loss rates to be positively correlated with size of juvenile chum salmon released arose for the 1.9 g right ventral (RV) clipped fish in 1984. Their residency half-life was 16 days, about the same as for 0.75 g fish released on the same day, and three times that of 1.9 g fish released in 1985 (Table 3). The significantly higher ($P < 0.01$, analysis of covariance) residency half-lives of fish released in 1984 than in other years may have arisen because these fish were released earlier in the spring. In other years, early release groups also had longer half-lives than later groups, but the slopes of the catch vs. time were not significantly different ($P > 0.05$).

Juvenile chum salmon actively maintained themselves in the bay. Residency half-lives of marked chum were 10–30 times longer than predicted from random loss with tidal flushing. Assuming that the mean intertidal volume of Netarts Bay is 75% of the total volume at MHW (Glanzman et al. 1971; Kreag 1979) and does not reenter the bay on subsequent tidal cycles, the half-life of water in Netarts Bay is <0.5 day.

Growth

Instantaneous growth rates in weight of fin-clipped chum salmon averaged 1.6–2.3% body weight per day (Table 3). No differences (analysis of covariance, $P > 0.05$) were found in growth in weight among these groups released within or among years. However, linear growth rates estimated from changes in fork length over time indicate that fish released at a smaller size grew more rapidly in 1984 (0.48 mm/d for 46 mm fish vs. 0.41 mm/d for 52 mm fish) and in 1986 (0.53 mm/d for 48 mm fish vs. 0.33 mm/d for 62 mm fish). Growth rates were similar for both 56 mm vs. 59 mm fish in 1985. Slopes derived from linear regression of mean individual lengths of all fish during a sampling period vs. elapsed time in days did not differ significantly ($P > 0.05$) from the rate of increase of lengths of marked fish in 1984, 1985, or 1986. These slopes were also similar among years. Increases in mean length probably reflected growth. None of the regressions of FL vs. time showed trends for decreasing size late in the spring that would be due to emigration of large individuals from the bay.

Biomass-Production

The biomass of juvenile chum salmon in Netarts Bay, estimated from population numbers (N_t) and average weight of the marked groups of fish during the week after release of

TABLE 2.—Estimates of the mean weight and length, of the population numbers based on marked fish, of the population biomass, and of the cumulative production of juvenile chum salmon in Netarts Bay, 1984–86.

	Average (g)	Average (mm)	Estimate number × 1000 (N_t)	biomass (kg)
1984				
17–18 April	1.6	56	610.5	977
19–20 April	1.6	56	468.0	772
23–24 April	1.9	59	429.6	816
26–27 April	1.8	58	176.6	323
2–3 May	1.9	58	150.3	280
10–11 May	2.1	62	71.1	151
16–17 May	2.1	62	65.9	141
23–24 May	2.9	62	28.6	84
30–31 May	3.2	71	34.2	109
Cumulative biomass (45 d)(kg)		13,591		
Instantaneous growth rate		0.02075		
Total production (kg)		282		
22–23 April	1.5	54	173.3	253
3–4 May	1.8	58	161.1	284
7–8 May	1.8	58	114.7	207
15–17 May	2.2	63	58.3	130
21–22 May	1.9	60	46.0	89
Cumulative biomass (19 d)(kg)		6,169		
Instantaneous growth rate		0.01675		
Total production (kg)		103		
1986				
1 May	0.8	45	947.4	805
5 May	1.0	47	444.5	449
8–9 May	1.1	49	392.6	440
13 May	1.4	53	240.0	331
15–16 May	1.4	53	317.3	444
21–3 May	1.7	57	171.1	294
28–29 May	1.9	60	63.4	122
7 June	2.6	65	30.6	78
12 June	2.6	66	5.3	14
Cumulative biomass (45 d)(kg)		11,154		
Instantaneous growth rate		0.0211		
Total production (kg)		235		

TABLE 3.—Data on the releases into Whiskey Creek, and the residency half-lives and growth rates of marked juvenile chum salmon in Netarts Bay, 1984–86.

Release data	Length at release (mm)	Weight at release (g)	Mark	Residency half-life (d)	Growth rate (% wt/d)
1984					
16 April	46	0.75	LV	14.94	2.27
16 April	58	1.9	RV	15.89	1.88
1985					
19 April	56	1.8	RV	5.54	1.61
26 April	59	1.9	LV	4.95	1.74
1986					
28–29 April	48	0.97	RV	7.38	2.26
11 May	62	2.2	RV + A	4.92	1.96
11 May	92	6.5	LV + A	<2.0	

both groups of marked hatchery fish, were estimated about 800–980 kg in 1984, 250–280 kg in 1985, and 450–800 kg in 1986 (Table 2). Increases in the biomass, indicative of accumulation of biomass from growth exceeding loss of biomass from migration or mortality, were not apparent in any year.

Total production or net growth of juvenile chum salmon (a product of the cumulative biomass over all days after the release of marked fish times the instantaneous growth rate of marked fish) measured 282 kg, 103 kg, and 235 kg in 1984, 1985, and 1986, respectively (Table 2). Total production is underestimated because production before the release of marked fish is not included. These production estimates are only 32%, 38%, and 37% of the estimated average biomass of the first two collection periods after releases in 1984, 1985, and 1986, respectively.

DISCUSSION

Netarts Bay is an important nursery area for juvenile chum salmon. Despite the small size and high flushing rate of Netarts Bay, juvenile chum salmon were captured during about a 2 mo duration in all three years. This is about the same duration as reported for wild juvenile chum salmon in Yaquina Bay, Oregon (Myers and Horton 1982), but is less than the three or more months reported for Tillamook Bay, Oregon (Henry 1953; Forsberg et al. 1977), Grays Harbor, Washington (Herrmann 1970), the Skagit River salt marsh, Washington (Congelton et al. 1982), and the Nanaimo Estuary, British Columbia (Healey 1979, 1982a). Juvenile chum salmon were reported in Hood Canal from January through July by Bax (1982). The mean residence times (see Healey 1979 for equation) of marked groups of hatchery-reared juvenile chum salmon (0.75–2.2 g at release) ranged from 5 to 23 days in Netarts Bay. These residence times are about the same as those found by Healey (1979) in the Nanaimo Estuary, but were more than the residence time of about 2 days in a small tidal channel reported by Congelton et al. (1982). Clearly, juvenile chum actively maintain themselves in many estuaries during early development.

Catches of juvenile chum salmon in the bay declined rapidly over time. The proportions lost from emigration and mortality are difficult to separate. Healey (1982a) concluded that some fish immediately emigrated from the Nanaimo and Nitinat Estuaries. Bax (1982) reported initial dispersal of marked hatchery fish, and net movements of 3–14 km/d for juvenile chum salmon in the elongated fjord of Hood Canal that would rapidly remove chum salmon from a small estuary. Lannan (1983) noted fish and bird predation on juvenile chum salmon in Netarts Bay. Most of the fish predation was caused by cutthroat trout, *Oncorhynchus clarki*, during downstream migration of chum fry and by Pacific staghorn sculpin, *Leptocottus armatus*, as fry entered the bay (J. Lannan, pers. comm.[3]). We examined 57 large (>100–215 mm FL) staghorn sculpin, 34 cutthroat trout (95–365 mm FL), and 28 coho salmon (95–156 mm FL) caught in our beach seine collections in Netarts Bay and found three juvenile chum salmon in staghorn sculpin stomachs and one in a coho salmon stomach. Gulls, mergansers, cormorants, and herons were common in the bay, but we have no data on their food habits. Harbor seals, *Phoca vitulina*, were also common in Netarts Bay in late spring; their scats were analyzed, but otoliths of juvenile salmon were not identified (Brown and Mate 1983), perhaps because the smallest sieve they used had a mesh size of 0.5 mm, a mesh that would retain otoliths of only large juvenile chum.

The distribution of juvenile chum salmon in Netarts Bay, with higher catches generally in the upper than lower bay early in the spring, and the reverse later in the spring is similar to that found by Healey (1979, 1982a) in the Nanaimo Estuary, by Myers and Horton (1982) in Yaquina Bay, and by Forsberg et al. (1977) in Tillamook Bay; but in the Nitinat Estuary no evidence of seaward progression was found (Healey 1982a). In Netarts Bay, juvenile chum salmon moved extensively over the tidal flats, aggregating in shallow water during periods of both high and low tide (cf. Mason 1974; Forsberg et al. 1977; Healey 1979, 1982a). In late spring, fish curtailed their movements into shallow warm waters of the upper bay at high tide and were concentrated instead in the lower estuary.

Based on limited pelagic sampling, we found no evidence for movement of fish into the deep channel areas of the lower bay later in the season. Juvenile chum salmon larger than 45–55 mm were caught in large numbers at some shallow seine stations in the lower bay in May and June. Some individuals were as large as 89

[3]J. Lannan, Oregon State University, Hatfield Marine Science Center, Newport, OR 97365, pers. commun. 22 December 1988.

mm and over 4 g wet weight. Fish averaged over 60 mm and 2 g by the end of May in all years (Table 2). Many juvenile chum salmon apparently stayed in shallow water in Netarts Bay beyond the size of 45–55 mm, the length at which they are thought to migrate from shallow estuarine waters into open neritic waters of other estuaries (Kaczyinski et al. 1973; Healey 1980a, 1982b; Simenstad and Salo 1980; Myers and Horton 1982). Large chum salmon apparently did not aggregate in the deep channels of Netarts Bay but emigrated directly out of the bay into open coastal waters.

The average size of juvenile chum salmon increased during their residence in Netarts Bay, as well as in Tillamook Bay (Forsberg et al. 1977), Yaquina Bay (Myers and Horton 1982), and Grays Harbor (Herrmann 1970). This increase suggests growth. Since large chum salmon are thought to emigrate more rapidly than small chum (Healey 1982a) and recruitment of downstream migrants may be prolonged, these estimates based on size-frequency distributions probably underestimate growth rates. The growth rates for marked chum salmon in Netarts Bay, 0.4–0.6 mm/d and 1.6–2.3% body weight (BW)/d, may also be underestimates if rapidly growing fish exit the bay sooner than slow growing fish. Growth rates of juvenile chum salmon in Netarts Bay are considerably less than the 1 mm/d and 6% BW/d estimated from marked juvenile chum in the Nanaimo Estuary (Healey 1979, 1982a) and the 8.6% BW/d for marked chum in Hood Canal (Bax and Whitmus 1981), but they are more similar to the 0.8 mm/d and about 4.2% BW/d for unmarked juvenile chum salmon in the Fraser River and Gulf Islands (Phillips and Barraclough 1978; Healey 1982b), the 2.7% BW/d for unmarked chum in Nitinat Lake, and the 0.4 mm/d found for unmarked chum in Steamer Bay, southeastern Alaska (Murphy et al. 1988). They are also similar to the growth rates of juvenile chum reared in saltwater aquaria at daily rations of 6–10% BW/d (Volk et al. 1984).

The cumulative biomass of juvenile chum salmon in Netarts Bay (13.6, 6.2, and 11.2 $\times$ 10^3 kg) was generally lower than the 14–66 $\times$ 10^3 kg estimated for naturally reared chum salmon in the similarly sized Nanaimo Estuary by Healey (1979). Total production of juvenile chum in the Nanaimo Estuary during the two years studied was 1,100–2,400 kg (or 0.2–0.4 g/m^2 of intertidal area), over an order of magnitude higher than that estimated in Netarts Bay (0.01–0.03 g/m^2 of intertidal area). This suggests that the carrying capacity of Netarts Bay for juvenile chum is limited. However, we found no evidence for density-dependent growth. Growth rates and residence times were about the same among years with several-fold differences in numbers of fry released and estimated biomass of juvenile chum salmon in the estuary (Tables 1, 2, 3). Production may be limited by the short residence times of large hatchery fish released late in the spring as well as by environmental factors other than direct competition for food.

Elevated water temperatures may affect growth of juvenile chum salmon, especially since Netarts Bay is at the southern extremity of the spawning range of this species in the northeastern Pacific Ocean. Kepshire (1971) reported an optimum temperature of 13°C for growth of juvenile chum salmon, and at 15°C, a temperature often recorded in Netarts Bay, food consumption was higher than at lower temperatures, but food conversion efficiency and growth were low. Irie (1984) found that ocean temperatures where juvenile chum salmon were found along the coast of Hokkaido were below 14°C. Juvenile chum salmon in Netarts Bay may also be excluded from the best foraging habitat by high temperatures. Densities of crustacean prey were highest in the intertidal areas of the upper bay (Chapman unpubl. data) where highest temperatures occurred. Costs of metabolism, food conversion, prey capture, and swimming may limit allocation of energy to growth when temperatures are above optimal (Brett 1979; Wissmar and Simenstad 1988).

Growth efficiencies may also be influenced by the quality and quantity of available prey. Small harpacticoid copepods (viz., *Harpacticus uniremis*) have been found to predominate the diet of juvenile chum salmon in estuaries (Healey 1979; Sibert 1979; Simenstad and Salo 1980; Simenstad and Wissmar 1984) where growth rates are high, whereas large amphipods predominated the diet in Netarts Bay (Chapman, unpubl. data), and mollusk larvae, hyperiid amphipods, and larvaceans were important prey for juvenile chum salmon in Steamer Bay, AK (Murphy et al. 1988) where growth was slower. Large prey, such as amphipods, may require more energy to capture because of highly developed escape responses (Volk et al. 1984), may be digested less efficiently because of their thick chitinous exoskeletons (Pandian 1967; Brett and Groves 1979), and may have lower per unit weight caloric value (Cummins and Wuycheck

1971) than smaller prey, such as harpacticoid copepods. Volk et al. (1984) reported that food conversion efficiency was much higher for juvenile chum salmon fed harpacticoid copepods than larger amphipods. All these factors could affect growth. Furthermore, pelagic calanoid copepods, hyperiid amphipods, and larvaceans, known to be important prey for large (>45 mm) juvenile chum salmon as they move to open neritic waters (Simenstad and Salo 1980), were not abundant in Netarts Bay, perhaps further constraining growth and production in this small estuary.

A possible strategy to circumvent the need for estuarine rearing where habitat quality limits production is to release juvenile chum salmon at a large size. Healey (1980a, 1982a) observed that seaward movement of juvenile chum salmon is size-dependent, with large fish moving offshore first. Juvenile chum salmon entering estuaries late in the spring also emigrate after a short time (Sibert et al. 1977; Ioka 1978). In Japan, juvenile chum salmon reared in salt water (Kobayashi 1980) migrate to the open sea within a week after release and chum salmon reared to a large size (8 g) return to hatcheries at a high rate (Ioka unpubl. data).

Our experimental releases of different sizes of fry indicate that large juvenile chum salmon do not utilize Netarts Bay as a nursery area. The large (6.5 g) chum we released in 1986 apparently migrated immediately to the ocean. When these fish returned to Whiskey Creek as adults in 1988 (presumably at age 3, based on the age structure of previous runs (Lannan 1983; J. Fisher unpubl. data)), the ratio of fish with missing left: right ventral fins was 2:1 (W. McNeil, pers. commun.[4]). This ratio was 0.6:1 in the juvenile chum salmon released in 1986 (Table 1). This suggests that these large (6.5 g) juvenile chum salmon that were not dependent on the estuary survived at rates that were 3–4 times higher than the smaller (1.0–2.2 g) fish released that year. More experiments are needed to confirm these results. Rearing chum salmon fry to a large size may be a useful method to enhance hatchery runs into estuaries, especially if size-selective predation is intensified by retarded growth owing to high temperatures or low availability of prey. Furthermore, large hatchery fish released late in the spring may have minimal adverse impacts on wild stocks.

[4]W. McNeil, Oregon State University, Hatfield Marine Science Center, Newport, OR 97365, pers. commun., 5 December 1988.

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Larval Fish Diets in Shallow Coastal Waters off San Onofre, California

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ABSTRACT: Stomach contents were analyzed from the larvae of six common coastal fish taxa (*Atherinopsis californiensis, Leuresthes tenuis, Paralabrax* spp., *Genyonemus lineatus, Seriphus politus,* and *Paralichthys californicus*) collected near San Onofre, California. Samples were collected at night at approximately monthly intervals between September 1978 and September 1979 during a study of ichthyoplankton distributions in these shallow coastal waters.

***Paralabrax* spp. and *Paralichthys californicus* larvae apparently did not feed at night, but high feeding incidences for the atherinids and especially the sciaenids suggested that these larvae did feed during early evening hours. Important components of the diets of all six taxa included the tintinnid genus *Stenosomella*, mollusc veligers, and especially the copepod *Euterpina acutifrons*.**

The vertical distributions of the fish larvae differed from the reported distributions of some of their principal prey taxa, suggesting that factors in addition to, or other than, specific feeding habits are important determinants in the nearshore distributions of fish larvae. The avoidance of seaward dispersal away from the relatively productive and stable nearshore zone may be an important factor influencing larval distribution.

Most studies on the feeding habits of fish larvae in the Southern California Bight have focused on species whose larvae occur primarily beyond the continental shelf, or are broadly distributed across the shelf and beyond (Arthur 1956, 1976; Hunter and Kimbrell 1980; Lasker 1975; Sumida and Moser 1980, 1984; Theilacker 1986). Larval fish feeding in the shallow coastal zone (depth ≤75 m) has, until recently, received relatively little attention. Lasker (1975, 1981) examined the requisite conditions for the successful first feeding of larval northern anchovy and suggested that the shallow nearshore zone may provide a better larval feeding environment than offshore waters, largely because of the more stable nature of the nearshore zone.

It has become increasingly apparent in recent years that this shallow nearshore zone is a unique area supporting distinctive, stable assemblages of fish larvae and zooplankters (Brewer et al. 1981, 1984; Gruber et al. 1982; Barnett et al. 1984; Brewer and Kleppel 1986; Petersen et al. 1986; Barnett and Jahn 1987; Walker et al. 1987). Feeding studies are beginning to be reported for some of the fish larvae that are largely restricted to this zone (Brewer and Kleppel 1986; Jahn et al. 1988).

The purpose of this report is to document the food habits of the larvae of six fish taxa in the shallow coastal waters off southern California. These six taxa include larvae occupying all levels of the water column: larval jacksmelt, *Atherinopsis californiensis*, and grunion, *Leuresthes tenuis*, are largely restricted to the neuston and upper water column; California halibut, *Paralichthys californicus*, and kelp and sand bass, *Paralabrax* spp., larvae occur throughout the water column but tend to be most abundant in midwater; and larval queenfish, *Seriphus politus*, and white croaker, *Genyonemus lineatus*, occur principally in the lower water column and epibenthos (Schlotterbeck and Connally 1982; Barnett et al. 1984; Jahn and Lavenberg 1986). All six taxa occur principally near shore throughout life (Frey 1971; Miller and Lea 1972; Barnett et al. 1984; Lavenberg et al. 1986;).

METHODS

Plankton samples were collected between 25 July 1978 and 23 September 1979 near San Onofre, CA (lat. 33°20′N, long. 117°30′W). The plankton sampling methodology and rationale are detailed by Barnett et al. (1984) and Walker et al. (1987) and are only briefly summarized here.

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Two sample sets, both of which provided complete water column coverage, were utilized in this study. A small sample set, used to make a rough approximation of feeding chronology, consisted of plankton samples collected twice during the day and twice at night within a 24 h period, on two occasions (25 July and 21 September 1978). These samples were collected along the 8 m isobath 1 km south of the San Onofre Nuclear Generating Station (SONGS) (July) and along the 13 m isobath just north of SONGS (September). A larger sample set, used to examine larval diets, consisted of plankton samples collected at night at approximately monthly intervals between 6 September 1978 and 23 September 1979, along a randomly selected isobath within each of five offshore blocks. These blocks were defined by depth contours: (A) 6–9 m, (B) 9–12 m, (C) 12–22 m, (D) 22–45 m, and (E) 45–75 m. The blocks were arrayed between 0.5 and 7.2 km from shore, approximately 1 km south of SONGS.

SONGS Unit 1, a 500 megawatt power plant, operated throughout the study period. Unit 1 has been shown to have had only very localized effects (Marine Review Committee 1979[1]) and it is unlikely to have influenced the results of this study.

Three different types of gear were used to collect both sample sets: a Brown Manta net (Brown and Cheng 1981), to sample the neuston (top 16 cm); a Brown-McGowan opening-closing bongo net, to sample the midwater column; and an Auriga net[2], to sample the epibenthos (within approximately 67 cm of the bottom). All three types of nets were constructed of 0.333 mm mesh Nitex[3], fitted with flowmeters, and towed at ca. 1 m/s to sample a target volume of 400 m^3. All samples were fixed in 10% seawater-formalin.

In the laboratory, the plankton samples were subsampled with a folsom plankton splitter and the fish larvae were sorted from the subsamples at 6–10× magnification under dissecting microscopes. Larvae utilized in the feeding studies were randomly selected from among those sorted from a subsample; a maximum of 100 specimens was selected from any subsample. These larvae were measured to the nearest 0.1 mm notochord or standard length, separated by developmental stage (preflexion = Pr; notochord flexion plus postflexion = FP), placed in a glycerin-water solution, and dissected with fine insect pins. The gut contents of each specimen were identified to the lowest possible taxon using a dissecting (50×) or compound (100–450×) microscope, as appropriate, and enumerated. The number of specimens dissected is listed by species, survey, and sample in Table 1.

Feeding incidence (%FI = percentage of larvae examined that contained at least one food item) was calculated with 95% confidence limits for each larval stage of each taxon. The 95% confidence limits were approximated as $\pm 1.96 (pq/n)^{1/2} + 1/2n$, where p = the proportion containing at least one food item, $q = 1 - p$, and n = the sample size. Percent frequency of occurrence (%FO) and percent of the total number (%N) of prey ingested by each larval fish stage were calculated for each prey type.

RESULTS

Feeding Chronology

Feeding incidence was calculated for *Seriphus politus*, *Paralabrax* spp., and *Paralichthys californicus* which were collected in the day/night sample sets in order to examine feeding chronology (Table 2). Larval *Genyonemus lineatus* and *Atherinopsis californiensis* did not occur in these samples, and too few *Leuresthes tenuis* were available to warrant examination.

During the day, 82% of the *S. politus* larvae contained at least one food item, while at night, 72% contained food. Feeding incidence increased from the morning through the evening, reaching a maximum of 94% for the larvae collected between 2003 and 2101 PST. However, since the feeding incidences were all quite high, and the 95% confidence limits about %FI broadly overlapped for all three morning through evening sampling episodes, it seems likely that there were no real differences in feeding incidence over this period. After midnight, feeding incidence was reduced to 33%, and the 95% confidence limits did not overlap with either the morning or evening values, indicating that feeding incidence indeed was reduced after midnight (Table 2).

Paralabrax spp. feeding incidence was 68%

[1]Marine Review Committee. 1979. Interim report of the Marine Review Committee to the California Coastal Commission part 1: General summary of findings, predictions, and recommendations concerning the cooling system of the San Onofre Nuclear Generating Station. Mar. Rev. Comm. Doc. 79–02, p. 1–20. Marine Review Committee of the California Coastal Commission, 631 Howard Street, San Francisco, CA 94105.

[2]MBC Applied Environmental Sciences, 947 Newhall Street, Costa Mesa, CA 92627.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Number of fish larvae dissected on each survey date. Pr = preflexion stage larvae; FP = flexion and postflexion stage larvae.

Survey date	*Atherinopsis californiensis*		*Leuresthes tenuis*		*Paralichthys californicus*		*Paralabrax spp.*		*Genyonemus lineatus*		*Seriphus politus*	
	Pr	FP	Pr	FP	Pr	FP	Pr	FP	Pr	FP	Pr	FP
1978												
06 Sept.	0	0	0	24	2	3	30	9	0	0	107	86
02 Oct.	1	0	0	10	15	1	0	0	39	4	13	26
01 Nov.	0	0	0	0	49	1	1	3	17	5	3	2
26 Dec.	2	5	0	0	31	7	0	0	89	33	0	0
1979												
29 Jan.	0	0	0	0	10	0	0	0	138	94	0	0
26 Feb.	2	31	0	0	41	2	0	0	146	98	0	0
26 Mar.	20	21	0	0	0	0	0	0	161	180	23	0
25 Apr.	7	19	7	13	0	0	0	0	40	86	18	0
23 May	0	8	17	20	0	0	0	0	32	49	19	14
25 June	1	1	22	95	0	0	0	0	0	2	51	66
24 July	0	0	0	0	0	0	43	8	0	0	74	14
22 Aug.	0	0	0	9	3	0	13	2	0	0	58	32
20 Sept.	0	0	2	14	35	9	24	2	9	0	87	49
Total	33	85	48	185	186	23	111	24	671	551	453	289

TABLE 2.—Feeding chronology of larval *Paralabrax* spp., *Paralichthys californicus*, and *Seriphus politus*. Survey A samples were collected at the 8 m isobath on 25 July 1978; Survey B samples were collected at the 13 m isobath on 21 September 1978. The time of day when samples were collected is given as Pacific Standard Time. N_t = total number of specimens dissected; N_f = number of specimens containing food; % FI = percent feeding incidence (100 × N_f); 95% confidence limits (C.L.) are given for % FI.

Survey	Time (PST)	*Paralabrax* spp.			*Paralichthys californicus*			*Seriphus politus*		
		N_t	N_f	% FI ± C.L.	N_t	N_f	% FI ± C.L.	N_t	N_f	%FI ± C.L.
A	0547–0626							34	26	76.5 ± 15.7
B	0920–1024	20	11	55.0 ± 24.3	17	9	52.9 ± 26.7			
A	1103–1153							37	32	86.5 ± 12.4
B	1345–1420	14	12	85.7 ± 21.9	7	0	0.0 ± 7.1			
B	1900–1958	18	9	50.0 ± 25.9	26	7	26.9 ± 19.0			
A	2003–2101							70	66	94.3 ± 6.1
B	2354–0049	24	0	0.0 ± 2.1	20	3	15.0 ± 18.1			
A	0118–0150							39	13	33.3 ± 16.1

during the day and 12% at night. Feeding incidence was highest (86%) during midafternoon (1345–1420 PST), dropped to 50% within an hour after sunset, and was 0% by about midnight (Table 2). The 95% confidence limits about %FI were rather broad owing to the small sample sizes, and it is unclear whether there were any real differences in feeding incidence from morning through early evening. However, the large differences in %FI and nonoverlapping confidence limits between the morning through evening and midnight sampling episodes do indicate a real reduction in feeding incidence at night.

Paralichthys californicus larvae displayed a low feeding incidence: 38% during the day and 22% at night. More larvae contained food items during midmorning that at any other time; none contained food in the midafternoon samples (but only seven larvae were available for disssection in the afternoon samples). At night, feeding incidence decreased from 27% about an hour after sunset to 15% by about midnight (Table 2). However, owing to the small sample sizes and consequent broad confidence limits about %FI, it is unclear whether there were any real differences in feeding incidence over this period.

Composition of the Diet

Atherinopsis californiensis

Larval jacksmelt were collected almost exclusively in the neuston in the two sampling blocks (A and B) between the 6 and 12 m isobaths, from October 1978 to June 1979. In total, 118 specimens were dissected (Table 1); 47% of these contained food. The overall feeding inci-

TABLE 3.—Feeding incidence of fish larvae by block, depth stratum, and larval developmental stage. Blocks correspond and E = epibenthos. N_t = total number of larvae dissected; N_f = number of larvae containing food;

Block	Stratum	Number of larvae	*Atherinopsis californiensis*		*Leuresthes tenuis*		*Paralichthys californicus*	
			Preflexion	Flexion-postflexion	Preflexion	Flexion-postflexion	Preflexion	Flexion-postflexion
A	N	N_t	17	60	11	91	3	4
		N_f	10	31	3	48	2	0
		%FI	58.8 ± 26.3	51.7 ± 13.5	27.3 ± 18.0	52.7 ± 10.8	66.7 ± 70.0	0.0 ± 12.5
	M	N_t	2	1	0	2	5	3
		N_f	2	1	0	1	4	0
		%FI	100.0 ± 25.0	100.0 ± 50.0	—	50.0 ± 94.3	80.0 ± 45.1	0.0 ± 16.7
	E	N_t	0	0	0	0	2	1
		N_f	0	0	0	0	1	0
		%FI	—	—	—	—	50.0 ± 94.3	0.0 ± 50.0
B	N	N_t	11	25	13	31	8	1
		N_f	5	6	10	13	4	0
		%FI	45.5 ± 34.0	24.0 ± 18.7	76.9 ± 26.8	41.9 ± 19.0	50.0 ± 40.9	0.0 ± 50.0
	M	N_t	0	0	0	0	13	0
		N_f	0	0	0	0	2	0
		%FI	—	—	—	—	15.4 ± 23.5	—
	E	N_t	0	0	0	0	2	2
		N_f	0	0	0	0	1	0
		%FI	—	—	—	—	50.0 ± 94.3	0.0 ± 25.0
C	N	N_t	0	2	7	21	10	1
		N_f	0	0	6	3	1	0
		%FI	—	0.0 ± 25.0	85.7 ± 33.1	14.3 ± 17.4	10.0 ± 23.6	0.0 ± 50.0
	M	N_t	0	0	0	0	31	6
		N_f	0	0	0	0	12	2
		%FI	—	—	—	—	38.7 ± 18.8	33.3 ± 46.1
	E	N_t	0	0	0	0	15	0
		N_f	0	0	0	0	5	0
		%FI	—	—	—	—	33.3 ± 27.2	—
D	N	N_t	0	0	8	12	14	0
		N_f	0	0	0	1	4	0
		%FI	—	—	0.0 ± 6.3	8.3 ± 19.8	28.6 ± 27.2	—
	M	N_t	0	0	0	0	47	2
		N_f	0	0	0	0	11	0
		%FI	—	—	—	—	23.4 ± 13.2	0.0 ± 25.0
	E	N_t	0	0	0	0	9	0
		N_f	0	0	0	0	5	0
		%FI	—	—	—	—	55.6 ± 38.0	—
E	N	N_t	0	0	9	28	3	0
		N_f	0	0	0	0	0	0
		%FI	—	—	0.0 ± 5.6	0.0 ± 1.8	0.0 ± 16.7	—
	M	N_t	0	0	0	0	19	3
		N_f	0	0	0	0	3	2
		%FI	—	—	—	—	15.8 ± 19.0	66.7 ± 70.0
	E	N_t	0	0	0	0	4	0
		N_f	0	0	0	0	0	0
		%FI	—	—	—	—	0.0 ± 12.5	—

dence was a little higher for the Pr larvae (56.7 ± 19.4%) than for the older specimens (43.2 ± 10.9%). Both the younger and older larvae displayed a higher feeding incidence in the block nearest shore (Table 3). For the FP larvae summed over all strata, the 95% confidence limits about %FI barely overlapped between block A (52.5 ± 13.4%) and those farther seaward (22.2 ± 17.5%). For the Pr larvae, however, confidence limits broadly overlapped between block

to isobaths: A = 6–9 m; B = 9–12 m; C = 12–22 m; D = 22–45 m; E = 45–75 m. Strata are N = neuston; M = midwater; %FI = feeding incidence (100 × N_f/N_t). Ninety-five percent confidence limits are given for %FI.

Block	Stratum	Number of larvae	*Paralabrax* spp.		*Genyonemus lineatus*		*Seriphus politus*	
			Preflexion	Flexion-postflexion	Preflexion	Flexion-postflexion	Preflexion	Flexion-postflexion
A	N	N_t	0	3	25	7	2	0
		N_f	0	1	19	7	2	0
		%FI	—	33.3 ± 70.0	76.0 ± 18.7	100.0 ± 7.1	100.0 ± 25.0	—
	M	N_t	0	0	41	11	49	1
		N_f	0	0	35	11	41	1
		%FI	—	—	85.4 ± 12.0	100.0 ± 4.5	83.7 ± 11.4	100.0 ± 50.0
	E	N_t	1	0	53	185	122	153
		N_f	0	0	50	176	98	117
		%FI	0.0 ± 50.0	—	94.3 ± 7.2	95.1 ± 3.4	80.3 ± 7.5	76.5 ± 7.0
B	N	N_t	0	3	26	1	2	0
		N_f	0	0	17	1	1	0
		%FI	—	0.0 ± 16.7	65.4 ± 20.2	100.0 ± 50.0	50.0 ± 94.3	—
	M	N_t	1	0	41	3	44	3
		N_f	0	0	41	3	29	2
		%FI	0.0 ± 50.0	—	100.0 ± 1.2	100.0 ± 16.7	65.9 ± 15.1	66.7 ± 70.0
	E	N_t	2	1	84	168	45	80
		N_f	0	0	83	153	40	62
		%FI	0.0 ± 25.0	0.0 ± 50.0	98.8 ± 2.9	91.1 ± 4.6	88.9 ± 10.3	77.5 ± 9.8
C	N	N_t	3	6	20	1	12	0
		N_f	0	1	16	1	7	0
		%FI	0.0 ± 16.7	16.7 ± 38.2	80.0 ± 20.0	100.0 ± 50.0	58.3 ± 32.0	—
	M	N_t	8	0	34	10	34	9
		N_f	5	0	29	10	23	8
		%FI	62.5 ± 39.8	—	85.3 ± 13.4	100.0 ± 5.0	67.7 ± 17.2	88.9 ± 26.1
	E	N_t	3	1	83	102	18	36
		N_f	1	0	81	102	12	33
		%FI	33.3 ± 70.0	0.0 ± 50.0	97.6 ± 3.9	100.0 ± 0.5	66.7 ± 24.6	91.7 ± 10.4
D	N	N_t	12	0	9	0	29	0
		N_f	0	0	4	0	11	0
		%FI	0.0 ± 4.2	—	44.4 ± 38.0	—	37.9 ± 19.4	—
	M	N_t	57	1	82	13	41	2
		N_f	3	0	79	13	32	2
		%FI	5.3 ± 6.7	0.0 ± 50.0	96.3 ± 4.7	100.0 ± 3.8	78.0 ± 13.9	100.0 ± 25.0
	E	N_t	5	0	128	50	11	5
		N_f	0	0	126	50	7	4
		%FI	0.0 ± 10.0	—	98.4 ± 2.6	100.0 ± 1.0	63.6 ± 33.0	80.0 ± 45.1
E	N	N_t	2	0	11	0	24	0
		N_f	0	0	10	0	12	0
		%FI	0.0 ± 25.0	—	90.9 ± 21.5	—	50.0 ± 22.1	—
	M	N_t	16	6	20	0	20	0
		N_f	7	5	20	0	17	0
		%FI	43.8 ± 27.4	83.3 ± 38.2	100.0 ± 2.5	—	85.0 ± 18.1	—
	E	N_t	1	3	14	0	0	0
		N_f	0	1	13	0	0	0
		%FI	0.0 ± 50.0	33.3 ± 70.0	92.9 ± 17.0	—	—	—

A and those farther seaward. The Pr larvae contained similar average numbers of prey items per feeding individual in blocks A and B (8.8 and 9.2 items per larva, respectively, summed over the water column), but the FP larvae contained nearly twice as many items in block A as in block B (Table 4).

The diet of the jacksmelt larvae varied little with location or over time: except in March 1979, the principal prey for all larval stages was the small harpacticoid copepod *Euterpina acutifrons*. In the March 1979 survey, the Pr larvae fed almost exclusively on *Labidocera trispinosa* nauplii. *Labidocera trispinosa* nauplii also were an appreciable fraction (36%) of the diet of the older jacksmelt larvae on this survey, although *E. acutifrons* still dominated. Minor components of the diet for the Pr larvae included centric diatoms (*Coscinodiscus* spp.), bivalve veligers, tintinnids (*Stenosomella* spp.), cirriped nauplii, and other copepods, e.g., *Paracalanus parvus* (Table 4). The FP larvae consumed all of these items as well, in addition to cirriped cypris larvae and a wider variety of copepods (e.g., *Oncea*, *Oithona*, *Corycaeus*).

Leuresthes tenuis

Larval grunion were collected almost exclusively from the neuston, in all five cross-shelf blocks, in September and Ocotber 1978 and April through September 1979. In total, 233 specimens were dissected (Table 1); 36% contained prey. Overall, feeding incidence differed little between the Pr stage larvae (39.6 ± 14.9%) and older larvae (35.7 ± 7.2%). The FP larvae displayed a

TABLE 4.—Diet of larval *Atherinopsis californiensis*. Results for preflexion stage larvae are given above; those for flexion-postflexion stage larvae are below. A blank column indicates that no larvae containing food occurred in that stratum. Since larval *A. californiensis* occurred only in the blocks A–C neuston and block A midwater, only those strata are shown. Water column strata are N = neuston; M = midwater. %N = the percent of the total food items attributable to a given category; %FO = the percent of the larvae containing food items that contained prey of the given category. Copepods listed as prey species include both copepodites and adults.

Block:	A (6–9 m)				B (9–12 m)		C (12–22 m)
Stratum:	N		M		N		N
Prey item	%N	%FO	%N	%FO	%N	%FO	%N
Preflexion							
Coscinodiscus spp.	1.4	10.0	0	0	0	0	
Stenosomella spp.	11.0	30.0	15.2	50.0	0	0	
Bivalve veligers	4.1	20.0	0	0	0	0	
Paracalanus parvus	0	0	3.0	50.0	0	0	
Labidocera trispinosa (nauplii)	52.1	40.0	0	0	97.8	100.0	
Euterpina acutifrons	19.2	50.0	27.3	100.0	2.2	20.0	
E. acutifrons (nauplii)	9.6	30.0	54.5	100.0	0	0	
Cirriped nauplii	2.7	20.0	0	0	0	0	
Total food items	73		33		46		0
Mean prey/feeding larva	7.3		16.5		9.2		0
Flexion-Postflexion							
Coscinodiscus spp.	4.7	6.5	0	0	8.1	16.7	
Stenosomella spp.	4.2	9.7	9.1	100.0	0	0	
Bivalve veligers	1.7	12.9	0	0	0	0	
Paracalanus parvus	0.8	6.5	27.3	100.0	0	0	
Labidocera trispinosa (nauplii)	1.7	3.2	0	0	35.1	33.3	
Oithona oculata	0.3	3.2	0	0	0	0	
Oncea spp.	0	0	0	0	2.7	16.7	
Euterpina acutifrons	79.9	80.6	54.5	100.0	40.5	16.7	
E. acutifrons (nauplii)	5.8	6.5	9.1	100.0	5.4	16.7	
Unidentified copepods	0.8	6.5	0	0	5.4	33.3	
Unidentified	0	0	0	0	2.7	16.7	
Total food items	359		11		37		0
Mean prey/feeding larva	11.6		11.0		6.2		0

clear gradient of feeding incidence from highest nearshore to lowest offshore (Table 3). Feeding incidence for the Pr larvae was highest between about 1 and 3.8 km from shore, and lower both seaward and shoreward, with no overlap of confidence limits (Table 3). Both the Pr and FP larvae consumed more items per feeding individual in the most nearshore block than elsewhere (Table 5). This was especially striking for the Pr larvae.

The most important prey for both the Pr and FP larvae was *Euterpina acutifrons* (Table 5). The Pr larvae tended to utilize *E. acutifrons* nauplii only a little less than the copepodites and adults, while the older larvae showed a clear preference for the copepodites and adults (Table 5). *Coscinodiscus* spp. were important in the diet of the Pr larvae, but constituted only a minor fraction of the FP diet. Minor components of the diet for the Pr larvae included dinoflagellates (*Peridinium* spp.), tintinnids (*Stenosomella* spp.), and small copepods (*Paracalanus parvus* and unidentified nauplii). Older larvae also consumed these items, as well as cirriped nauplii, bivalve veligers, and a wider variety of copepods (e.g., *Oncea, Oithona, Microsetella,* and *Corycaeus*).

TABLE 5.—Diet of larval *Leuresthes tenuis*. Results for preflexion stage larvae are given above; those for flexion-postflexion stage larvae are below. A blank column indicates that no larvae containing food occurred in that stratum. Since larval *L. tenuis* occurred only in the neuston and midwater, only those strata are shown. Water column strata are N = neuston; M = midwater. %N = the percent of the total food items attributable to a given category; %FO = the percent of the larvae containing food items that contained prey of the given category. Copepods listed as prey species include both copepodites and adults.

Block:	A (6–9 m)				B (9–12 m)			C (12–22 m)			D (22–45 m)			E (45–75 m)	
Stratum:	N		M		N		M	N		M	N		M	N	M
Prey item	%N	%FO	%N	%FO	%N	%FO	%N	%N	%FO	%N	%N	%FO	%N	%N	%N
Preflexion															
Coscinodiscus spp.	33.3	33.3			0	0		0	0						
Peridinium spp.	3.0	33.3			0	0		0	0						
Stenosomella spp.	6.1	33.3			0	0		0	0						
Euterpina acutifrons	36.4	66.7			17.4	30.0		57.1	66.7						
E. acutifrons (nauplii)	18.1	33.3			0	0		0	0						
Unidentified copepods	3.0	33.3			65.2	80.0		0	0						
Unidentified copepod nauplii	0	0			13.0	10.0		0	0						
Unidentified Crustacea	0	0			0	0		28.6	33.3						
Unidentified	0	0			4.3	10.0		14.3	16.7						
Total food items	33		0		23		0	7		0	0		0	0	0
Mean prey/feeding larva	11.0		0		2.3		0	1.2		0	0		0	0	0
Flexion-postflexion															
Coscinodiscus spp.	1.9	10.0	0	0	0	0		0	0		0	0			
Peridinium spp.	0.1	2.1	0	0	0	0		0	0		0	0			
Stenosomella spp.	2.0	10.0	0	0	0	0		0	0		0	0			
Bivalve Veligers	0.1	2.1	0	0	0	0		0	0		0	0			
Acartia tonsa	0	0	100.0	100.0	0	0		0	0		0	0			
Paracalanus parvus	1.4	10.0	0	0	0.8	7.7		0	0		0	0			
Oithona oculata	0	0	0	0	9.2	15.4		0	0		0	0			
Corycaeus anglicus	0.3	2.1	0	0	0	0		0	0		0	0			
Oncea spp.	1.0	6.3	0	0	0	0		0	0		0	0			
Euterpina acutifrons	62.5	66.7	0	0	82.4	76.9		100.0	100.0		100.0	100.0			
E. acutifrons (nauplii)	15.5	37.5	0	0	0	0		0	0		0	0			
Microsetella rosea	0.1	2.1	0	0	0	0		0	0		0	0			
Unidentified copepods	13.2	20.8	0	0	4.2	38.5		0	0		0	0			
Ciiriped nauplii	0.3	4.2	0	0	0	0		0	0		0	0			
Unidentified	1.6	20.8	0	0	3.4	30.8		0	0		0	0			
Total food items	699		1		119		0	21		0	3		0	0	0
Mean prey/feeding larva	14.6		1.0		9.2		0	7.0		0	3.0		0	0	0

Paralichthys californicus

Two hundred and nine larval California halibut were examined from samples collected between September 1978 and February 1979, and in August and September 1979 (Table 1). Most larvae (89%) were Pr stage. The overall 28% feeding incidence was comparable to the 22% nighttime incidence noted in the day/night sample set. Although the feeding incidence for the Pr larvae was nearly 70% higher than that of the FP larvae (29.5 ± 6.9% vs. 17.4 ± 17.7%), it was well within the 95% confidence limits about the FP value. The Pr larvae displayed a higher feeding incidence in the most nearshore block, but only the confidence limits about the %FI values for the most nearshore and seaward blocks failed to overlap (block A: 70.0 ± 33.4%; block E: 11.5 ± 14.2%). The highest feeding incidence for the FP larvae occurred in the 45–75 m depth block, but all confidence limits broadly overlapped owing to the small sample sizes (Table 3). Among the FP larvae, all four specimens that contained food were collected in midwater. Pr larvae in the nearshore blocks typically contained more prey items per individual than did larvae in the most offshore blocks (Table 6).

Larval California halibut consumed few types of prey. Bivalve veligers, *Euterpina acutifrons* nauplii, the tintinnid genus *Stenosomella*, and unidentified material (including unidentified invertebrate eggs, and setae—presumably from polychaete larvae) accounted for most of the diet of the Pr larvae (Table 6). Young larvae consumed a narrower range of prey types near shore than they did farther seaward. Most of the diet near shore was composed of *Stenosomella* spp., while seaward of the 12 m isobath, *Euterpina acutifrons* nauplii, unidentified material, and bivalve veligers constituted the bulk of the diet. The few FP larvae with gut contents contained only unidentifiable material (Table 6).

Paralabrax spp.

Due to the difficulty and uncertainty in separating larval kelp and sand basses, identification was only to the level of genus. A total of 135 larval *Paralabrax* spp. were examined from samples collected between September and November 1978 and between July and Septem-

TABLE 6.—Diet of larval *Paralichthys californicus*. Results for preflexion stage larvae are given above; those for the column strata are N = neuston; M = midwater; E = epibenthos. %N = the percent of the total food items attributable to listed as prey species include both copepodites and adults.

Block:	A (6–9 m)						B (9–12 m)					
Stratum:	N		M		E		N		M		E	
Prey item	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO
Preflexion												
Rhizosolenia spp.	0	0	0	0	0	0	0	0	0	0	0	0
Peridinium spp.	0	0	0	0	0	0	0	0	0	0	0	0
Radiolaria	0	0	0	0	0	0	0	0	0	0	0	0
Stenosomella spp.	90.9	100.0	90.6	25.0	100.0	100.0	77.3	25.0	98.2	50.0	0	0
Bivalve veligers	9.1	50.0	0	0	0	0	0	0	0	0	0	0
Euterpina acutifrons (nauplii)	0	0	0	0	0	0	0	0	1.8	50.0	0	0
Unidentified copepods	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified nauplii	0	0	0	0	0	0	0	0	0	0	100.0	100.0
Unidentified	0	0	9.4	75.0	0	0	22.7	75.0	0	0	0	0
Total food items	11		32		23		22		55		2	
Mean prey/feeding larva	5.5		8.0		23.0		5.5		27.5		2.0	
Flexion-postflexion												
Unidentified												
Total food item	0		0		0		0		0		0	
Mean prey/feeding larva	0		0		0		0		0		0	

ber 1979, mainly in midwater, seaward of the 12 m isobath (Table 1). Most of the larvae were Pr stage (82%). Eighteen percent of the larvae dissected contained food, similar to the 21% nighttime average noted in the day/night comparison. There was no clear cross-shelf pattern in feeding incidence (Table 3), but a vertical pattern may have been suggested by the lower incidence in the neuston (3.4 ± 8.3%) and higher incidences in midwater (22.5 ± 9.2%) and epibenthos (13.3 ± 20.5%). Although the average feeding incidence for the Pr larvae (14.7 ± 1.1%) was less than half that for the FP larvae (33.3 ± 20.9%), it still was contained within the broad confidence bounds about the FP value.

Tintinnids, bivalve veligers, and copepods were among the most important prey for larval *Paralabrax* spp. (Table 7). Unidentified items (including invertebrate eggs and setae—presumably from polychaete larvae) constituted the major dietary component for the Pr larvae. However, tintinnids (*Stenosomella* spp.) and bivalve veligers also were important. The FP larvae tended to consume larger items, especially copepods (e.g., *Acartia tonsa Euterpina acutifrons*, and *Oithona oculata*). Both the Pr and the FP larvae typically contained few prey items (Table 7).

Genyonemus lineatus

A total of 1,222 larval white croaker were examined from samples collected between October 1978 and June 1979, and in September 1979 (Table 1). Fifty-five percent of the larvae were Pr stage. Nearly all of the larvae contained food: feeding incidence was 92.8% (±2.0%) for the Pr larvae and 95.6% (±1.0%) for the FP larvae. Feeding incidence was high in all strata and all cross-shelf blocks (Table 3). For both larval stage categories, feeding incidence in the neuston was distinctly lower (75.0 ± 4.8%) than it was in midwater (94.5 ± 1.6%) and epibenthos (96.2 ± 0.7%). There was little evidence of a cross-shelf gradient in feeding incidence for either stage category (Table 3).

Larval white croaker consumed a wide variety of prey types (Tables 8, 9). Pr larvae tended to eat smaller items, particularly tintinnids, bivalve and gastropod veligers, and small copepods, especially all stages of *Euterpina acutifrons* (Table 8). The FP larvae consumed these

flexion-postflexion stage larvae are below. A blank column indicates that no larvae contained food occurred in that stratum. Water a given food category; %FO = the percent of larvae containing food items that contained prey of the given category. Copepods

Block:	C (12–22 m)						D (22–45 m)						E (45–75 m)			
Stratum:	N		M		E		N		M		E		N	M		E
Prey item	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%N	%FO	%N
Preflexion																
Rhizosolenia spp.	0	0	1.7	8.3	0	0	0	0	0	0	0	0		0	0	
Peridinium spp.	0	0	1.7	8.3	0	0	0	0	3.3	9.1	0	0		0	0	
Radiolaria	0	0	0	0	0	0	0	0	3.3	9.1	0	0		0	0	
Stenosomella spp.	0	0	5.0	8.3	0	0	0	0	0	0	0	0		0	0	
Bivalve veligers	0	0	1.7	8.3	8.3	20.0	20.0	50.0	16.7	9.1	50.0	20.0		0	0	
Euterpina acutifrons (nauplii)	0	0	78.3	58.3	50.0	80.0	70.0	75.0	36.7	36.4	20.0	20.0		0	0	
Unidentified copepods	0	0	0	0	16.7	20.0	0	0	0	0	0	0		33.3	33.3	
Unidentified nauplii	0	0	0	0	0	0	0	0	0	0	0	0		0	0	
Unidentified	100.0	100.0	11.7	58.3	25.0	40.0	10.0	25.0	40.0	90.9	30.0	60.0		66.7	66.7	
Total food items	1		60		12		10		30		10		0	3		0
Mean prey/feeding larva	1.0		5.0		2.4		2.5		2.7		2.0		0	1.0		0
Flexion-postflexion																
Unidentified			100.0	100.0										100.0	100.0	
Total food item	0		2		0		0		0		0		0	2		0
Mean prey/feeding larva	0		1.0		0		0		0		0		0	1.0		0

TABLE 7.—Diet of larval *Paralabrax* spp. Results for preflexion stage larvae are given above; those for the flexion-postflexion stage larvae are below. A blank column indicates that no larvae contained food in that stratum. Water column strata are N = neuston; M = midwater; E = epibenthos. %N = the percent of the total food items attributable to a given food category; %FO = the percent of larvae containing food items that contained prey of the given category. Copepods listed as prey include both copepodites and adults.

Block:	A (6–9 m)				B (9–12 m)			C (12–22 m)					
Stratum:	N		M	E	N	M	E	N		M		E	
Prey item	%N	%FO	%N	%N	%N	%N	%N	%N	%FO	%N	%FO	%N	%FO
Preflexion													
Stenosomella spp.										43.8	20.0	0	0
Bivalve veligers										6.3	20.0	0	0
Paracalanus parvus										0	0	0	0
Euterpina acutifrons										12.5	20.0	0	0
E. acutifrons (nauplii)										6.3	20.0	0	0
Unidentified copepods										0	0	0	0
Cirriped nauplii										6.3	20.0	0	0
Unidentified										25.0	80.0	100.0	100.0
Total food items	0	0	0	0	0	0	0	0		16		2	
Mean prey/feeding larva	0	0	0	0	0	0	0	0		3.2		2.0	
Flexion-postflexion													
Acartia tonsa	0	0						100.0	100.0				
Corycaeus anglicus	0	0						0	0				
Oithona oculata	0	0						0	0				
Euterpina acutifrons	0	0						0	0				
Unidentified copepods	0	0						0	0				
Euphausid calyptopis	0	0						0	0				
Unidentified	100.0	100.0						0	0				
Total food items	1	0	0	0	0	0	0	1		0		0	
Mean prey/feeding larva	1.0	0	0	0	0	0	0	1.0		0		0	

Block:	D (22–45 m)				E (45–75 m)				
Stratum:	N	M		E	N	M		E	
Prey item	%N	%N	%FO	%N	%N	%N	%FO	%N	%FO
Preflexion									
Stenosomella spp.		0	0			0	0		
Bivalve veligers		80.0	67.7			9.1	14.3		
Paracalanus parvus		0	0			18.2	14.3		
Euterpina acutifrons		0	0			0	0		
E. acutifrons (nauplii)		0	0			0	0		
Unidentified copepods		20.0	33.3			0	0		
Cirriped nauplii		0	0			0	0		
Unidentified		0	0			72.7	85.7		
Total food items	0	5		0	0	11		0	
Mean prey/feeding larva	0	1.7		0	0	1.6		0	
Flexion-postflexion									
Acartia tonsa						14.3	20.0	0	0
Corycaeus anglicus						0	0	33.3	100.0
Oithona oculata						42.9	20.0	0	0
Euterpina acutifrons						14.3	20.0	33.3	100.0
Unidentified copepods						14.3	20.0	33.3	100.0
Euphausid calyptopis						14.3	20.0	0	0
Unidentified						0	0	0	0
Total food items	0	0		0	0	7		3	
Mean prey/feeding larva	0	0		0	0	1.4		3.0	

small items as well, but in addition consumed larger items such as larger copepod species and mysids (Table 9). Cross-shelf patterns in dietary composition were apparent; for example, tintinnids in the Pr diet shifted from *Stenosomella* spp. near shore to predominantly *Condonaria* spp. farthest from shore (Table 8). Pr larvae also tended to consume more bivalve veligers more frequently in the blocks farthest from shore, but more gastropod veligers nearer shore (Table 8). The FP larvae likewise consumed most gastropod veligers nearer shore, but did not display clear evidence of a cross-shelf pattern in the consumption of bivalve veligers (Table 9). The average number of prey items consumed by the Pr larvae ranged from 2.9 to 8.8 per feeding individual (Table 8), while for the FP larvae the number of items consumed ranged from 2.0 to 8.3 (Table 9). Cross-shelf patterns in the number of items consumed were not apparent. The FP larvae contained more prey items per feeding individual in midwater and epibenthos than in the neuston. There were no consistent differences between strata for the Pr larvae or between midwater and epibenthos samples for the older larvae (Tables 8, 9).

Seriphus politus

A total of 742 larval queenfish (61% Pr stage) were examined from samples collected between September and November 1978 and between March and September 1979 (Table 1). The overall 67% feeding incidence was comparable to the 72% night incidence noted in the day/night sample set. Feeding incidence differed little between the Pr larvae (73.5 ± 4.2%) and the FP larvae (79.2 ± 4.8%). Relatively few larvae were available for dissection from the neuston samples, and overall these larvae displayed the lowest feeding incidence (48.5 ± 12.6% for the Pr larvae; no FP larvae occurred in the neuston). Feeding incidence differed little between midwater (76.4 ± 6.1%) and epibenthos (79.4 ± 3.8%). The feeding incidence for the Pr larvae was highest in block A (81.5 ± 6.1%) where larval abundance was highest, and ranged between about 62 and 68% in the remaining blocks. Confidence limits about the means for blocks B (63.1 ± 9.4%) and D (61.7 ± 11.2%) did not overlap the confidence limits about the mean for block A, but those about the means for blocks C (66.7 ± 12.4%) and E (65.9 ± 15.1%) did overlap the confidence limits about the block A mean. The lowest feeding incidences for the FP larvae occurred in blocks A (76.6 ± 7.0%) and B (77.1 ± 9.6%) where larval abundance was highest, and the highest feeding incidences occurred in blocks C (91.1 ± 9.4%) and D (85.7 ± 33.1%) where larval abundance was low. However, the confidence bounds about these estimates overlapped in all cases.

Larval queenfish consumed a wide variety of prey types (Tables 10, 11). Pr larvae consumed mainly small items, especially bivalve veligers and small copepods such as *Paracalanus parvus* and *Euterpina acutifrons* (Table 10). The FP larvae also consumed these small items in addition to larger items, especially mysids and gammarid amphipods (Table 11). Cross-shelf patterns in dietary composition and number of items consumed were not clear. For the Pr larvae, feeding specimens contained fewer prey items per individual in block E than elsewhere (Table 10), but for the FP larvae no pattern was apparent (Table 11). Both the Pr and FP larvae tended to consume slightly more prey items per feeding individual in midwater than in epibenthos. Smaller prey contributed larger fractions of the diet in midwater than in the epibenthos for both larval stage classes.

DISCUSSION

Both the limited day/night sample series and the much larger night-only sample set indicated that larvae contained food well into the night. A nonzero feeding incidence does not necessarily imply recent feeding, however, but only indicates the presence of food in the gut. For example, a slow digestion and evacuation rate might result in the appearance of nocturnal feeding even if the larvae in fact were not feeding. On the other hand, a low feeding incidence does not necessarily imply nonfeeding, especially for taxa that have a straight gut, since these larvae frequently void their gut contents during capture and fixation (June and Carlson 1971; Hay 1981). Hunter (1981) noted that fish larvae are visual feeders lacking rods and retinomotor pigment migration (e.g., Blaxter 1968) and are probably largely restricted to feeding in daylight hours. The low feeding incidences noted for larval *Paralabrax* spp. in the night samples suggests that they do feed only during the day. Similarly, *Paralichthys californicus* larvae may feed only during the day, although their day-night differences in feeding incidence were smaller and less convincing owing to the broad confidence limits about the %FI values. Both

TABLE 8.—Diet of preflexion stage larvae of *Genyonemus lineatus*. A blank column indicates that no larvae contained food in that stratum. Water column strata are N = neuston; M = midwater; E = epibenthos. %N = the percent of the total food items attributable to a given food category; %FO = the percent of the larvae containing food items that contained prey of the given category. Copepods listed as prey species include both copepodites and adults.

Block:	A (6–9 m)						B (9–12 m)						C (12–22 m)					
Stratum:	N		M		E		N		M		E		N		M		E	
Prey item	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO
Coscinodiscus spp.	0	0	0	0	0	0	0	0	0	0	0.6	2.4	0	0	0	0	0.9	4.9
Peridinium spp.	3.8	10.5	0.7	2.9	0	0	1.3	5.9	2.0	9.8	0.1	1.2	0	0	3.6	10.3	1.1	4.9
Radiolaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stenosomella spp.	37.7	10.5	43.3	25.7	4.4	8.0	21.8	23.5	18.1	24.4	0.6	1.2	0	0	0.7	3.4	0	0
Condonaria spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Bivalve veligers	6.6	26.3	4.6	17.1	3.2	8.0	12.8	35.3	8.3	31.7	7.5	20.5	5.4	6.3	3.6	13.8	9.4	24.7
Gastropod veligers	2.8	15.8	1.3	8.6	0.6	2.0	3.8	17.6	3.1	7.3	1.7	6.0	0	0	1.5	6.9	1.1	6.2
Spionidae	0	0	0	0	0	0	0	0	0	0	0.3	1.2	0	0	0	0	0	0
Polychaete trochophores	0	0	0.3	2.9	5.7	18.0	0	0	0.4	2.4	0.6	2.4	1.8	6.3	1.5	6.9	1.1	6.2
Cyphonautes, uniden.	0	0	0	0	0	0	0	0	0	0	0.6	1.2	0	0	0	0	0.2	1.2
Penilia avirostris	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cladocerans, uniden.	0	0	0	0	0	0	1.3	5.9	0	0	0	0	0	0	0	0	0	0
Paracalanus parvus	0	0	3.9	17.1	10.1	18.0	0	0	0.4	2.4	1.7	7.2	0	0	0	0	1.1	4.9
Oithona oculata	0	0	1.0	8.6	1.3	4.0	1.3	5.9	0	0	5.8	14.5	0	0	2.2	3.4	2.5	6.2
O. oculata nauplii	0	0	0	0	0	0	0	0	0.4	2.4	1.7	6.0	0	0	2.2	6.9	0.9	4.9
Corycaeus anglicus	0	0	0	0	1.3	4.0	0	0	0.4	2.4	0.9	3.6	0	0	0	0	6.2	16.0
Oncea spp.	0	0	0.3	2.9	0	0	0	0	0	0	0.9	3.6	0	0	1.5	3.4	3.9	4.9
Euterpina acutifrons	16.1	36.8	18.9	60.0	27.8	48.0	17.9	35.3	15.7	61.0	38.9	42.2	5.4	18.8	24.1	44.8	32.5	64.2
E. acutifrons nauplii	6.6	15.8	13.0	28.6	7.6	12.0	15.4	23.5	25.2	39.0	2.9	9.6	46.4	50.0	17.5	34.5	12.1	29.6
Microsetella rosea	0	0	0.3	2.9	0	0	5.1	17.6	3.9	14.6	3.5	8.4	0	0	9.5	20.7	10.5	19.8
M. rosea nauplii	0	0	0	0	0	0	0	0	0.8	4.9	0	0	0	0	0	0	0.2	1.2
Longipedia spp. nauplii	1.9	10.5	0	0	0	0	3.8	11.8	3.1	9.8	0	0	3.6	12.5	2.9	10.3	1.6	8.6
Copepods, unidentified	0	0	0	0	12.7	18.0	0	0	0.8	2.4	5.2	9.6	3.6	6.3	2.9	10.3	1.6	4.9
Copepod nauplii, uniden.	0	0	0	0	0.6	2.0	0	0	0	0	0	0	0	0	0	0	0.5	1.2
Ostracods, uniden.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Cumaceans, uniden.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Euphausids, calyptopis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified	24.5	78.9	12.4	60.0	24.6	46.0	15.4	58.8	17.3	48.8	26.5	55.4	33.9	68.8	26.3	58.6	12.4	44.4
Total food items	106		307		158		78		254		347		56		137		437	
Mean prey/feeding larva	5.6		8.8		3.2		4.6		6.2		4.2		3.5		4.7		5.4	

TABLE 8.—*Continued.*

Block:	D (22–45 m)						E (45–75 m)					
Stratum:	N		M		E		N		M		E	
Prey item	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO
Coscinodiscus spp.	0	0	1.0	3.8	0.9	2.4	0	0	0	0	0	0
Peridinium spp.	0	0	8.0	13.9	0.6	2.4	6.9	10.0	6.4	25.0	0	0
Radiolaria	0	0	0.5	1.3	0	0	0	0	0	0	0	0
Stenosomella spp.	0	0	0	0	0	0	0	0	3.8	5.0	3.6	7.7
Condonaria spp.	0	0	1.5	5.1	0	0	24.1	30.0	5.1	20.0	0	0
Bivalve veligers	22.7	25.0	40.5	62.0	19.4	35.7	24.1	50.0	19.2	60.0	16.4	38.5
Gastropod veligers	0	0	0.8	3.8	1.2	5.6	0	0	0	0	0	0
Spionidae	0	0	0	0	0	0	0	0	0	0	0	0
Polychaete trochophores	0	0	0	0	0.6	3.2	0	0	2.6	10.0	1.8	7.7
Cyphonautes, uniden.	0	0	0.5	2.5	0.5	1.6	0	0	0	0	0	0
Penilia avirostris	0	0	0	0	0.2	0.8	0	0	0	0	0	0
Cladocerans, uniden.	0	0	0	0	0	0	0	0	0	0	0	0
Paracalanus parvus	0	0	0	0	0.5	2.4	0	0	0	0	0	0
Oithona oculata	0	0	0	0	2.9	9.5	0	0	0	0	0	0
O. oculata nauplii	4.5	25.0	1.5	7.6	0	0	0	0	0	0	0	0
Corycaeus anglicus	0	0	0.5	2.5	1.7	5.6	0	0	0	0	0	0
Oncea spp.	0	0	1.5	5.1	0.8	3.2	0	0	3.8	10.0	3.6	15.4
Euterpina acutifrons	4.5	25.0	21.6	39.2	57.9	80.2	0	0	0	0	1.8	7.7
E. acutifrons nauplii	13.6	50.0	10.3	22.8	1.2	4.0	3.4	10.0	5.1	10.0	0	0
Microsetella rosea	13.6	25.0	5.0	16.5	3.5	9.5	0	0	2.6	10.0	0	0
M. rosea nauplii	0	0	0	0	0	0	13.8	40.0	2.6	10.0	5.5	15.4
Longipedia spp. nauplii	22.7	25.0	0	0	0	0	3.4	10.0	0	0	0	0
Copepods, unidentified	0	0	0	0	0.6	2.4	0	0	1.3	5.0	0	0
Copepod nauplii, uniden.	0	0	0.5	1.3	0	0	3.4	10.0	1.3	5.0	0	0
Ostracods, uniden.	0	0	0	0	0.2	0.8	0	0	0	0	1.8	7.7
Cumaceans, uniden.	0	0	0	0	0.2	0.8	0	0	0	0	0	0
Euphausids, calyptopis	0	0	0	0	0.5	2.4	0	0	0	0	0	0
Unidentified	18.2	50.0	6.3	15.2	6.6	23.8	20.7	60.0	46.2	65.0	65.5	61.5
Total food items	22		398		648		29		78		55	
Mean prey/feeding larva	5.5		5.0		5.1		2.9		3.9		4.2	

TABLE 9.—Diet of flexion-postflexion stage larvae of *Genyonemus lineatus*. Since none of these larvae occurred in block Water column strata are N = neuston; M = midwater; E = epibenthos. %N = the percent of the total food items the given category. Copepods listed as prey include both copepodites and adults.

Block:	A (6–9 m)						B (9–12 m)					
Stratum:	N		M		E		N		M		E	
Prey item	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO
Coscinodiscus spp.	0	0	0	0	0.2	0.6	0	0	6.3	33.3	0	0
Rhizosolenia spp.	0	0	0	0	0.1	0.6	0	0	0	0	0	0
Peridinium spp.	0	0	0	0	0	0	0	0	0	0	0	0
Radiolaria	0	0	0	0	0	0	0	0	0	0	0	0
Sagitta spp.	0	0	0	0	0.4	1.1	0	0	0	0	0.2	1.3
Bivalve veligers	6.3	14.3	9.1	63.6	2.3	7.4	0	0	0	0	5.8	19.0
Gastropod veligers	12.5	28.6	1.3	9.1	0.5	2.3	0	0	0	0	1.9	5.2
Spionidae	6.3	14.3	1.3	9.1	0.5	2.3	0	0	0	0	0	0
Polychaete larvae	0	0	9.1	27.3	2.3	5.7	0	0	6.3	33.3	9.5	26.1
Membranipora spp. cyphonautes	0	0	0	0	0.1	0.6	0	0	0	0	0.1	0.7
Cyphonautes, uniden.	0	0	0	0	0.8	4.0	0	0	0	0	1.0	3.9
Penilia avirostris	0	0	0	0	0.2	1.1	0	0	0	0	0	0
Acartia tonsa	0	0	0	0	0.1	0.6	0	0	0	0	2.1	9.8
Paracalanus parvus	37.5	28.6	32.5	63.6	54.1	48.9	0	0	18.8	66.7	29.5	51.0
Labidocera trispinosa	0	0	1.3	9.1	4.5	9.7	0	0	12.5	33.3	1.2	4.6
Pontellopsis spp.	0	0	0	0	0	0	0	0	0	0	2.6	7.8
Candacia spp.	0	0	0	0	0	0	0	0	0	0	0	0
Oithona oculata	0	0	3.9	27.3	1.1	3.4	0	0	0	0	0.6	2.6
O. oculata nauplii	0	0	0	0	0	0	0	0	0	0	0	0
O. plumifera	0	0	0	0	0	0	0	0	0	0	0.2	1.3
Corycaeus anglicus	0	0	2.6	9.1	0.6	2.3	0	0	0	0	1.1	5.9
Oncea spp.	0	0	0	0	0.2	1.1	0	0	0	0	0.3	2.0
Euterpina acutifrons	18.8	42.9	31.2	81.8	12.0	30.1	0	0	50.0	100.0	30.3	54.2
E. acutifrons nauplii	6.3	14.3	0	0	1.7	6.3	0	0	0	0	0.2	1.3
Microsetella rosea	0	0	0	0	0.1	0.6	0	0	0	0	0.3	2.0
Longipedia spp. nauplii	0	0	0	0	0.1	0.6	0	0	0	0	0	0
Copepods, uniden.	0	0	0	0	11.3	32.4	0	0	0	0	4.3	14.4
Copepod nauplii, uniden.	6.3	14.3	1.3	9.1	0	0	0	0	0	0	0	0
Cirriped nauplii	0	0	0	0	0.1	0.6	0	0	0	0	0.5	2.0
Cirriped cypris	0	0	0	0	0.1	0.6	0	0	0	0	0.2	1.3
Nebalia spp.	0	0	1.3	9.1	0	0	0	0	0	0	0.1	0.7
Ostracods, uniden.	0	0	0	0	0	0	0	0	0	0	0.1	0.7
Metamysidopsis elongata	0	0	0	0	0	0	0	0	0	0	0.1	0.7
Mysidopsis californica	0	0	0	0	0	0	0	0	0	0	0.3	2.0
M. intii	0	0	0	0	0	0	0	0	0	0	0.2	0.7
Neomysis rayii	0	0	0	0	0	0	0	0	0	0	0.3	2.0
Neomysis spp. juveniles	0	0	0	0	1.4	5.1	0	0	0	0	0.3	1.3
Siriella pacifica	0	0	0	0	0	0	0	0	0	0	0.1	0.7
Mysids, uniden.	0	0	0	0	0.8	2.3	0	0	0	0	0.7	3.9
Gammarids, uniden.	0	0	0	0	1.4	5.7	0	0	0	0	0.3	2.0
Euphausids, calyptopis	0	0	0	0	0.1	0.6	0	0	0	0	0	0
Caridean zoeae	0	0	0	0	0.1	0.6	0	0	0	0	0	0
Brachyuran zoeae	0	0	0	0	0	0	0	0	0	0	0.1	0.7
Brachyuran megalopae	0	0	0	0	0.1	0.6	0	0	0	0	0	0
Fish larvae	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified	6.3	14.3	5.2	27.3	2.6	9.1	100.0	100.0	6.3	33.3	5.0	24.8
Total food items	16		77		844		2		16		884	
Mean prey/feeding larva	2.3		7.0		4.8		2.0		5.3		5.8	

E, that block is not included on the table. A blank column indicates that no larvae contained food in that stratum. attributable to a given food category; %FO = the percent of the larvae containing food items that contained prey of

Block:	C (22–45 m)						D (45–75 m)				
Stratum:	N		M		E		N	M		E	
Prey item	%N	%FO	%N	%FO	%N	%FO	%N	%N	%FO	%N	%FO
Coscinodiscus spp.	0	0	0	0	0.5	2.9		0	0	0.6	4.0
Rhizosolenia spp.	0	0	0	0	0	0		0	0	0	0
Peridinium spp.	0	0	0	0	0.6	2.0		0	0	0.3	2.0
Radiolaria	0	0	0	0	0.1	1.0		0	0	0	0
Sagitta spp.	0	0	0	0	0	0		0	0	0.3	2.0
Bivalve veligers	0	0	7.4	30.0	2.1	12.7		6.2	23.1	4.5	22.0
Gastropod veligers	0	0	3.7	20.0	1.2	9.8		0	0	2.9	18.0
Spionidae	0	0	0	0	0	0		0	0	0.3	2.0
Polychaete larvae	0	0	0	0	6.1	25.5		0	0	0.3	2.0
Membranipora spp. cyphonautes	0	0	0	0	0	0		0	0	0	0
Cyphonautes, uniden.	0	0	0	0	0.5	2.0		0	0	0.3	2.0
Penilia avirostris	0	0	0	0	0	0		0	0	0	0
Acartia tonsa	0	0	0	0	0	0		0	0	0	0
Paracalanus parvus	0	0	7.4	30.0	18.0	37.3		0	0	1.9	6.0
Labidocera trispinosa	0	0	0	0	0	0		0	0	0	0
Pontellopsis spp.	0	0	0	0	4.0	18.6		0	0	0	0
Candacia spp.	0	0	1.9	10.0	0	0		0	0	0	0
Oithona oculata	0	0	9.3	10.0	0.7	5.9		4.9	7.7	4.2	10.0
O. oculata nauplii	0	0	0	0	0.2	2.0		1.2	7.7	0	0
O. plumifera	0	0	1.9	10.0	0	0		0	0	0	0
Corycaeus anglicus	0	0	1.9	10.0	6.3	28.4		1.2	7.7	4.2	16.0
Oncea spp.	0	0	27.8	50.0	15.2	33.3		2.5	7.7	1.0	4.0
Euterpina acutifrons	33.3	100.0	29.6	40.0	31.4	61.8		65.4	92.3	70.2	86.0
E. acutifrons nauplii	0	0	0	0	0	0		9.9	15.4	0.3	2.0
Microsetella rosea	0	0	3.7	20.0	2.4	12.7		1.2	7.7	1.6	8.0
Longipedia spp. nauplii	0	0	0	0	0	0		0	0	0	0
Copepods, uniden.	66.7	100.0	0	0	1.3	4.9		0	0	2.9	10.0
Copepod nauplii, uniden.	0	0	0	0	3.8	2.0		0	0	0	0
Cirriped nauplii	0	0	0	0	0	0		0	0	0	0
Cirriped cypris	0	0	0	0	0	0		0	0	0	0
Nebalia spp.	0	0	0	0	0	0	0	0	0	0	0
Ostracods, uniden.	0	0	0	0	0	0	0	0	0	0.3	2.0
Metamysidopsis elongata	0	0	0	0	0	0	0	0	0	0	0
Mysidopsis californica	0	0	0	0	0	0		0	0	0	0
M. intii	0	0	0	0	0	0		0	0	0	0
Neomysis rayii	0	0	0	0	0.5	3.9		0	0	1.0	6.0
Neomysis spp. juveniles	0	0	0	0	0	0		0	0	0	0
Siriella pacifica	0	0	0	0	0	0		0	0	0	0
Mysids, uniden.	0	0	0	0	0	0		0	0	0	0
Gammarids, uniden.	0	0	0	0	0	0		0	0	0	0
Euphausids, calyptopis	0	0	0	0	0.2	2.0		1.2	7.7	0	0
Caridean zoeae	0	0	0	0	0.2	2.0		0	0	0	0
Brachyuran zoeae	0	0	0	0	0.1	1.0		0	0	0	0
Brachyuran megalopae	0	0	0	0	0	0		0	0	0	0
Fish larvae	0	0	0	0	0.1	1.0		0	0	0	0
Unidentified	0	0	5.6	20.0	4.0	25.5		6.2	23.1	2.6	14.0
Total food items	3		54		846		0	81		309	
Mean prey/feeding larva	3.0		5.4		8.3		0	6.2		6.2	

TABLE 10.—Diet of preflexion stage larvae of *Seriphus politus*. A blank column indicates that no larvae contained food in that stratum. Water column strata are N = neuston; M = midwater; E = epibenthos. %N = the percent of the total food items attributable to a given food category; %FO = the percent of the larvae containing food items that contained prey of the given category. Copepods listed as prey include both copepodites and adults.

Block:	A (6–9 m)						B (9–12 m)						C (12–22 m)					
Stratum:	N		M		E		N		M		E		N		M		E	
Prey item	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%FO
Radiolaria	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Stenosomella spp.	0	0	0	0	0	0	0	0	20.0	10.3	0	0	20.5	14.3	12.3	13.0	0	0
Condonaria spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tintinnids, uniden.	0	0	4.2	7.3	0	0	0	0	1.4	3.4	0	0	0	0	0	0	0	0
Bivalve veligers	7.7	50.0	7.1	19.5	3.0	8.2	0	0	2.9	3.4	1.5	7.5	7.7	28.6	8.6	30.4	4.8	16.7
Gastropod veligers	0	0	1.8	7.3	1.7	4.1	0	0	1.4	3.4	0.5	2.5	0	0	0	0	2.4	8.3
Polychaete larvae	0	0	0	0	0	0	0	0	1.4	3.4	0	0	0	0	0	0	0	0
Evadne nordmanni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Acartia tonsa	0	0	0	0	0.3	1.0	0	0	0	0	0	0	0	0	2.5	8.7	0	0
Paracalanus parvus	0	0	6.5	22.0	17.2	31.6	0	0	4.3	10.3	5.4	25.0	0	0	0	0	2.4	8.3
Oithona oculata	0	0	5.4	4.9	8.9	14.3	0	0	5.7	3.4	1.5	7.5	2.6	14.3	22.2	17.4	0	0
O. plumifera	0	0	0	0	0	0	0	0	0	0	0.5	2.5	0	0	0	0	2.4	8.3
Corycaeus anglicus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.4	8.3
Euterpina acutifrons	0	0	56.0	75.6	46.8	55.1	0	0	41.4	69.0	69.8	82.5	5.1	14.3	6.2	21.7	45.2	33.3
E. acutifrons nauplii	69.2	50.0	4.8	14.6	0.6	2.0	0	0	2.9	6.9	0.5	2.5	41.0	28.6	21.0	21.7	11.9	33.3
Microsetella rosea	0	0	0	0	0	0	0	0	0	0	1.0	5.0	0	0	0	0	0	0
M. rosea nauplii	0	0	0	0	0	0	0	0	0	0	0	0	2.6	14.3	0	0	0	0
Copepods, uniden.	0	0	1.8	7.3	10.0	23.5	0	0	7.1	13.8	3.9	17.5	5.1	28.6	7.4	21.7	7.1	16.7
Copepod nauplii, uniden.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.5	8.7	0	0
Longipedia spp. nauplii	15.4	100.0	1.8	7.3	0	0	0	0	0	0	0	0	0	0	4.9	8.7	0	0
Holmesimysis costata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.4	8.3
Neomysis spp., juveniles	0	0	0	0	0.3	1.0	0	0	0	0	0	0	0	0	0	0	0	0
Mysids, uniden.	0	0	0	0	0.6	2.0	0	0	0	0	0.5	2.5	0	0	0	0	0	0
Cumaceans, uniden.	0	0	0	0	0	0	0	0	0	0	0.5	2.5	0	0	0	0	2.4	8.3
Gammarids, uniden.	0	0	0	0	0.8	3.1	0	0	0	0	0	0	0	0	0	0	7.1	16.7
Crustaceans, uniden.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Unidentified	7.7	50.0	10.7	43.9	10.0	35.7	100.0	100.0	11.4	27.6	14.6	75.0	15.4	57.1	12.3	43.5	9.5	33.3
Total food items	13		168		361		1		70		205		39		81		42	
Mean prey/feeding larva	6.5		4.1		3.7		1.0		2.4		5.1		5.6		3.5		3.5	

TABLE 10.—*Continued.*

Block:	D (22–45 m)						E (45–75 m)				
Stratum:	N		M		E		N		M		E
Prey item	%N	%FO	%N	%FO	%N	%FO	%N	%FO	%N	%F	%N
Radiolaria	0	0	0	0	0	0	0	0	3.0	5.9	
Stenosomella spp.	0	0	14.2	18.8	0	0	42.9	16.7	12.1	11.8	
Condonaria spp.	0	0	1.5	6.3	0	0	0	0	0	0	
Tintinnids, uniden.	0	0	0	0	0	0	0	0	0	0	
Bivalve veligers	12.1	18.2	25.4	37.5	0	0	0	0	27.3	29.4	
Gastropod veligers	0	0	0.7	3.1	0	0	0	0	0	0	
Polychaete larvae	3.0	9.1	0	0	0	0	0	0	0	0	
Evadne nordmanni	0	0	0.7	3.1	0	0	0	0	0	0	
Acartia tonsa	0	0	0.7	3.1	0	0	0	0	0	0	
Paracalanus parvus	12.1	18.2	1.5	6.3	0	0	0	0	0	0	
Oithona oculata	0	0	20.9	21.9	5.9	14.3	0	0	3.0	5.9	
O. plumifera	0	0	0	0	0	0	0	0	0	0	
Corycaeus anglicus	0	0	0	0	0	0	0	0	0	0	
Euterpina acutifrons	27.3	18.2	5.2	18.8	5.9	14.3	4.8	8.3	0	0	
E. acutifrons nauplii	0	0	1.5	6.3	5.9	14.3	0	0	3.0	5.9	
Microsetella rosea	0	0	0	0	0	0	0	0	0	0	
M. rosea nauplii	0	0	0	0	0	0	0	0	0	0	
Copepods, uniden.	18.2	36.4	5.2	18.8	41.2	42.9	0	0	0	0	
Copepod nauplii, uniden.	3.0	9.1	0	0	17.6	14.3	0	0	6.1	11.8	
Longipedia spp. nauplii	0	0	0	0	0	0	0	0	0	0	
Holmesimysis costata	0	0	0	0	0	0	0	0	0	0	
Neomysis spp., juveniles	0	0	0	0	0	0	0	0	0	0	
Mysids, uniden.	0	0	0.7	3.1	0	0	0	0	0	0	
Cumaceans, uniden.	0	0	0	0	0	0	0	0	0	0	
Gammarids, uniden.	0	0	0	0	0	0	0	0	0	0	
Crustaceans, uniden.	0	0	0	0	0	0	4.8	8.3	0	0	
Unidentified	24.2	54.5	21.6	40.6	23.5	57.1	47.6	83.3	45.5	54.7	
Total food items	33		134		17		21		33		0
Mean prey/feeding larva	3.0		4.2		2.4		1.8		1.9		0

TABLE 11.—Diet of flexion-postflexion stage larvae of *Seriphus politus*. A blank column indicates that no column strata are N = neuston; M = midwater; E = epibenthos. %N = the percent of the total food items prey of the given category. Copepods listed as prey include both copepodites and adults.

Block:	A (6–9 m)					B (9–12 m)				
Stratum:	N	M		E		N	M		E	
Prey item	%N	%N	%FO	%N	%FO	%N	%N	%FO	%N	%FO
Sagitta spp.		0	0	0.5	0.9		0	0	0.6	1.6
Bivalve veligers		0	0	0.5	0.9		0	0	0	0
Gastropod veligers		0	0	0	0		0	0	0.6	1.6
Polychaete larvae		0	0	2.6	4.3		0	0	3.1	8.1
Cyphonautes, uniden.		0	0	0	0		0	0	0	0
Evadne nordmanni		0	0	0	0		20.0	50.0	0	0
Acartia tonsa		0	0	8.3	8.5		0	0	3.7	9.7
Paracalanus parvus		0	0	1.6	2.6		0	0	12.3	14.5
Labidocera trispinosa		0	0	0	0		0	0	0.6	1.6
Pontellopsis spp.		0	0	3.6	4.3		0	0	0	0
Oithona oculata		50.0	100.0	1.0	1.7		0	0	0	0
Corycaeus anglicus		0	0	0.5	0.9		0	0	0	0
Oncea spp.		0	0	1.0	0.9		0	0	0	0
Euterpina acutifons		0	0	14.6	13.7		20.0	50.0	32.5	25.8
Microsetella rosea		0	0	0.5	0.9		0	0	0	0
Copepods, uniden.		0	0	9.4	9.4		60.0	100.0	9.8	11.3
Cirriped nauplii		0	0	0	0		0	0	0.6	1.6
Holmesimysis costata		0	0	4.2	6.0		0	0	0.6	1.6
Metamysidopsis elongata		0	0	2.6	3.4		0	0	0	0
Neomysis rayii		0	0	4.2	6.8		0	0	4.9	12.9
Siriella pacifica		0	0	0	0		0	0	1.2	1.6
Mysids, uniden.		12.5	100.0	14.6	19.7		0	0	11.7	25.8
Gammarids, uniden.		12.5	100.0	18.2	22.2		0	0	5.5	14.5
Caridean zoeae		0	0	3.1	5.1		0	0	0.6	1.6
Callianassa spp. zoeae		0	0	0	0		0	0	1.2	3.2
Crustaceans, uniden.		0	0	2.6	4.3		0	0	0.6	1.6
Unidentified		25.0	100.0	6.3	10.3		0	0	9.8	24.2
Total food items	0	8		192		0	5		163	
Mean prey/feeding larva	0	8.0		1.6		0	2.5		2.6	

taxa develop a coil in the gut during the preflexion stage, reducing the likelihood that the low night feeding incidences reflected voiding of the gut contents during capture. The *Paralabrax* spp. feeding incidence was relatively high in the day samples, further suggesting that voiding of the gut contents did not contribute appreciably to the low feeding incidence observed at night.

The higher night feeding incidences for the remaining species, especially *Genyonemus lineatus* and *Seriphus politus*, suggest that they may have continued to feed after dark, at least during the early evening hours. Bagarinao and Hunter (1983) noted that older (≥10 mm) *Engraulis mordax* larvae feed in the dark if prey densities are high enough, and suggested that the full moon provides sufficient illumination for these larvae to feed near the surface at lower prey densities. Other reports of apparent larval fish feeding at night include, for example, Brewer and Kleppel's (1986) report of high feeding incidence until midnight for larval *G. lineatus* collected near shore in Santa Monica Bay, and the reports of Sumida and Moser (1980) and Jenkins (1987) that larval *Merluccius productus* off southern California and *Rhombosolea tapirina* in Port Phillip Bay, Australia, respectively, had high feeding incidences throughout much of the day and night. Brewer and Kleppel (1986) and Sumida and Moser (1980) attributed the high night feeding incidences in their studies to slow digestion rather than to nocturnal feeding, and this cannot be discounted as an alternative explanation for the high nocturnal feeding incidences noted in the present study. This alternative interpretation may be supported by the observation that feeding incidences tended to be lower during the August and September 1979

larvae contained food in that stratum. Block E is not shown because no larvae occurred there. Water attributable to a given food category; %FO = the percent of the larvae containing food items that contained

Block:	C (12–22 m)					D (22–45 m)				
Stratum:	N	M		E		N	M		E	
Prey item	%N	%N	%FO	%N	%FO	%N	%N	%FO	%N	%FO
Sagitta spp.		0	0	0	0		0	0	0	0
Bivalve veligers		0	0	0	0		0	0	0	0
Gastropod veligers		0	0	0	0		0	0	0	0
Polychaete larvae		0	0	0	0		0	0	0	0
Cyphonautes, uniden.		0	0	1.9	3.0		0	0	0	0
Evadne nordmanni		0	0	0	0		0	0	0	0
Acartia tonsa		52.6	50.0	11.1	12.1		0	0	0	0
Paracalanus parvus		0	0	1.9	3.0		0	0	0	0
Labidocera trispinosa		0	0	7.4	9.0		0	0	0	0
Pontellopsis spp.		0	0	1.9	3.0		0	0	0	0
Oithona oculata		0	0	0	0		0	0	0	0
Corycaeus anglicus		0	0	3.7	6.0		0	0	0	0
Oncea spp.		0	0	0	0		0	0	0	0
Euterpina acutifons		0	0	5.6	9.0		0	0	0	0
Microsetella rosea		0	0	0	0		0	0	0	0
Copepods, uniden.		15.8	25.0	5.6	6.0		100.0	100.0	0	0
Cirriped nauplii		0	0	0	0		0	0	0	0
Holmesimysis costata		0	0	5.6	9.0		0	0	0	0
Metamysidopsis elongata		0	0	1.9	3.0		0	0	0	0
Neomysis rayii		0	0	1.9	3.0		0	0	0	0
Siriella pacifica		0	0	0	0		0	0	0	0
Mysids, uniden.		15.8	37.5	13.0	21.2		0	0	25.0	25.0
Gammarids, uniden.		15.8	25.0	27.8	24.2		0	0	25.0	25.0
Caridean zoeae		0	0	0	0		0	0	0	0
Callianassa spp. zoeae		0	0	0	0		0	0	0	0
Crustaceans, uniden.		0	0	0	0		0	0	0	0
Unidentified		0	0	11.1	18.2		0	0	50.0	50.0
Total food items	0	19		54		0	6		4	
Mean prey/feeding larva	0	2.4		1.6		0	3.0		1.0	

surveys. In both cases, sampling was mainly after midnight, in contrast to all other surveys when sampling was mainly before midnight. The potential influence of moonlight on feeding incidence could not be addressed in this study, since all samples were collected within five days of new moon. However, as noted above, the study by Bagarinao and Hunter (1983) suggests that nocturnal feeding is possible during full moon, at least near the surface.

Cross-shelf differences in feeding incidence were apparent for 5 of the 12 stage-taxon categories examined; for 4 of these, feeding incidence was higher near shore and lower in seaward blocks. This may reflect a higher level of feeding intensity near shore, but since the nearshore blocks were always sampled earlier than the offshore blocks during each survey, the alternative explanation that these patterns merely reflected the cessation of larval feeding at night cannot be dismissed. The results for *Atherinopsis californiensis*, and perhaps for *Leuresthes tenuis*, are more likely to represent real, but small-scale differences in feeding incidence since these two species were collected mainly in the two or three shallowest blocks, and relatively little time elapsed between samples.

The composition of the larval diets described in this study is similar to the diet described for many larval marine teleosts (e.g., Arthur 1976; Sumida and Moser 1980; Hunter 1981) in that major fractions were contributed by copepod nauplii and copepodites. In the present study, the harpacticoid copepod *Euterpina acutifrons* was an important component of the diets of all six taxa examined. This copepod species has not been noted in other studies as being such an important dietary component and the reason for

its importance at San Onofre is unknown. *Euterpina acutifrons* may be more abundant near San Onofre than elsewhere (mean density 10,640/m^3—range 1,078–37,314/m^3—between the 9 and 100 m isobaths during a microzooplankton study conducted at San Onofre during the year prior to the feeding study), or it might have been unusually abundant during the year when the feeding studies were done, but appropriate data from long-term and larger scale studies that would allow evaluation of these suggestions are unavailable. Other particularly important copepods were the cyclopoid *Oithona oculata* and the calanoid *Labidocera trispinosa*. However, copepods were not the only important food items in the nearshore zone and were not the dominant prey for some of the Pr stage larvae. Other consistently important prey included tintinnids, especially *Stenosomella* spp., and mollusc veligers (principally bivalves, but also gastropods in some cases). Older sciaenid larvae consumed appreciable numbers of mysids. The diets of the older larvae did not exclude small items such as mollusc veligers or copepod nauplii; instead, the small items continued to be consumed, and larger items such as larger copepod species (e.g., Barnett and Jahn 1987: table 3) were added as well. This is consistent with Hunter's (1981) observation that although the maximum prey size selected increases more or less rapidly with increasing larval fish size, the minimum prey size increases very slowly. Thus larger larvae can select from among a wider range of prey sizes, consuming the energetically more valuable larger items when those are available, and perhaps maintaining on smaller items when large prey are unavailable (Hunter 1976; Hunter and Kimbrell 1980).

Concurrent plankton sampling that would allow comparisons of the spatial distributions of the fish larvae and their prey species was not part of the present study. However, other studies did examine the distribution and abundance of the zooplankton during the day in the same area from 1977 through 1980 (Barnett and Jahn 1987), and spatial patterns of the fish larvae and their prey can be compared in a general way on the basis of these studies. The majority of the most important prey categories occurred in highest concentrations near shore (e.g., Barnett and Jahn 1987). For example, *Oithona oculata* was most abundant in the epibenthos shoreward of the 13 m isobath (Barnett and Jahn 1987), while *Paracalanus parvus* was abundant throughout the water column shoreward of the 30 m isobath (Fig. 1). The Marine Review Committee's unpublished count data, from samples collected at San Onofre on 31 October 1978 indicated that *Euterpina acutifrons* nauplii were approximately 4–34 times more abundant in samples taken at the 9, 13, and 30 m isobaths than in samples from the 100 m isobath (maximum abundance 141,200/m^3, averaged over the water column at 13 m), while the copepodites and adults were 1.5–19 times more abundant at the shallow stations than at the 100 m station (maximum abundance 11,600/m^3, averaged over the water column at 13 m). *Labidocera trispinosa* nauplii were restricted to the very nearshore zone, shoreward of the 13 m isobath, where they occurred throughout the water column (Fig. 1). Bivalve veligers were abundant throughout the water column between the 13 and 30 m isobaths, while gastropod veligers occurred throughout the nearshore zone and seaward to at least the 100 m isobath (Fig. 1). The most frequently occurring mysid taxa in the larval diets—*Holmesimysis costata*, *Neomysis rayii*, and *Neomysis* spp. juveniles—all were most abundant in the epibenthos shoreward of the 15 m isobath (Bernstein and Gleye 1981[4]). Clutter (1967) reported that *H. costata*, as well as several other mysid species, was restricted to the nearshore zone off La Jolla, CA.

Barnett et al. (1984) described the cross-shelf and vertical distributions of the larvae of five of the six fish taxa considered here. All five were most abundant shoreward of the 45 m isobath; larvae of the sixth taxon, *Paralabrax* spp., occur principally shoreward of the 36 m isobath (Lavenberg et al. 1986). The atherinid larvae are almost exclusively neustonic; *Paralichthys californicus* and the *Paralabrax* spp. larvae occur throughout the water column (especially in midwater); and the *Genyonemus lineatus* and *Seriphus politus* larvae are located mainly in the lower water column and epibenthos (Schlotterbeck and Connally 1982; Barnett et al. 1984; Jahn and Lavenberg 1986). Ontogenetic redistributions occur during the larval phase for at least some of the taxa: the flexion and postflexion stage larvae of *G. lineatus* and *S. politus* are more nearshore and epibenthic than the preflexion stage larvae (Barnett et al. 1984), while the transforming postflexion larvae of *Paralichthys californicus* occur most frequently and in

[4]Bernstein, B. B. and L. G. Gleye. 1981. The ecology of mysids in the San Onofre region. Volume II: New reports. Rep. Mar. Rev. Comm., Rep. No. MEC01281999.

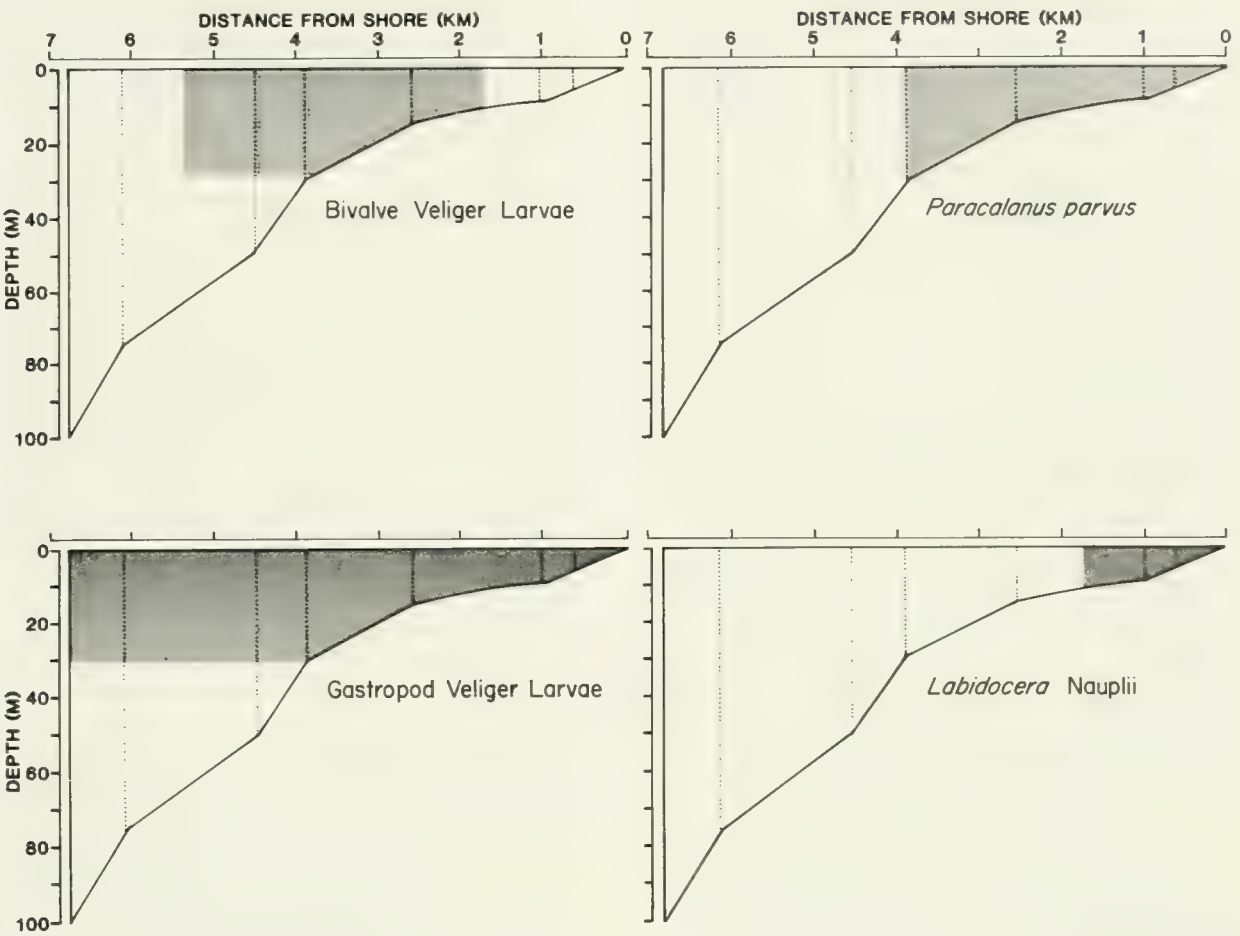

FIGURE 1.—Zones of significantly higher concentration of four zooplankton taxa near SONGS. Shaded areas represent higher concentration as determined by nonparametric one-way ANOVA ($P < 0.05$) on number per m^3 data. Redrawn from Marine Review Committee Document 78-01, Annual report to the California Coastal Commission, September 1977–August 1978: Updated estimated effects of SONGS Unit 1 on marine organisms. August 1978.

highest abundance in the neuston shoreward of the 9 m isobath.

Thus the distributions of the fish larvae and their prey are broadly similar. However, the sharp vertical gradients in abundance patterns for the atherinids and the older sciaenid larvae apparently do not closely match the vertical patterns of their prey. In discussing the results of their respective larval fish feeding studies, both of which utilized concurrent larval fish and zooplankton sampling during the day and night, Brewer and Kleppel (1986) and Jahn et al. (1988) remarked on this lack of a close match between the vertical distributions of fish larvae and their prey in the shallow nearshore zone. They suggested that factors other than, or in addition to, feeding must be important in determining larval distributions in the nearshore zone. Avoidance of dispersal seaward, away from the shallow coastal zone, is likely to be one of the most important factors (e.g., Brewer and Kleppel 1986).

Nearshore currents off southern California are mainly parallel to shore, tend to reverse at roughly tidal frequency, and have only a weak cross-shelf component (e.g., Winant and Bratkovich 1981; Jackson 1986). A comparison of the variances of the longshore and cross-shelf current speeds off San Onofre (the variance of the current speed is a good measure of the energy of the coastal current) indicates that the variance of the longshore current (102 cm^2/s^2) is about four times that of the cross-shelf current (25 cm^2/s^2) (Elwany et al. in press). This stronger longshore current has a net southerly motion, while the weak cross-shelf current has a net shoreward motion (Marine Review Committee 1977[5]). Thus

[5]Marine Review Committee. 1977. Annual report to the California Coastal Commission, August 1976—August 1977, summary of the estimated effects on marine life of Unit 1,

plankters occupying the nearshore zone in the San Onofre vicinity will, on average, tend to be transported alongshore, but not out of the nearshore zone. Those plankters occupying the epibenthos, where currents are minimal, are especially likely to be retained in the nearshore zone (e.g., Barnett et al. 1984; Jahn and Lavenberg 1986; Barnett and Jahn 1987). At times, the nearshore plankton distributions at San Onofre are disrupted (Barnett and Jahn 1987), and during those times the neritic fish larvae may be transported seaward.

Tidal mixing and nutrient recycling in the nearshore zone allows high rates of phytoplankton production near shore (Petersen et al. 1986; Barnett and Jahn 1987). This production can be utilized directly by fish larvae (e.g., Lasker 1975, 1981), or indirectly in the form of microzooplankton and small macrozooplankton, both of which occur in high concentrations near shore (e.g., Lasker 1978; Barnett and Jahn 1987). The nearshore zone appears to provide a good feeding environment for fish larvae, on average. However, it appears that this resource is largely utilized only by the nearshore species, since the larvae of more offshore species are relatively rare in the shallow coastal waters (e.g., Gruber et al. 1982; Barnett et al. 1984). Lasker (1975) demonstrated that the food resources of the nearshore zone may be critical to the first-feeding larvae of the broadly distributed species *Engraulis mordax*, and Theilacker (1986) showed that first-feeding larval *Trachurus symmetricus*, a more offshore species, were less vulnerable to starvation in nearshore habitats around the islands off the California coast than they were in offshore waters. However, larval *T. symmetricus* are uncommon in shallow coastal waters and in general there is little evidence that the shallow coastal zone provides an important feeding resource for the larvae of offshore fish species.

The observations that the larvae of the offshore fish species apparently make little use of the food resources of the nearshore zone, and that among the larvae of the neritic species the distributions of the larvae and their prey do not closely correspond, suggest that food is not the primary influence in determining nearshore larval fish distributions. What the primary influence (or influences) is remains to be determined. It does seem reasonable to conclude, at least, that larval fish distributions within the nearshore zone are a function of the advantages conferred by remaining in this environment.

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Seasonal Differences in Spawning, Egg Size, and Early Development Time of the Hawaiian Anchovy or Nehu, *Encrasicholina purpurea*[1]

Thomas A. Clarke

ABSTRACT: Nehu spawning is concentrated in a 1 hour period shortly after sunset; the delay after sunset is longer in the winter than in summer. Incubation time for nehu eggs is 22–35 hours and is inversely related to temperature. Development time between hatching and first feeding shows relatively greater seasonal differences, and total embryonic development time during the coldest months is almost twice that of the warmest months. Nehu egg size is inversely related to temperature. The seasonal differences in egg size are probably the result of a physiological response to temperature. The potential adaptive value of the seasonal change in egg size in this tropical species is more likely related to size-specific differences in predation rates rather than to seasonal changes in abundance or size of food for larvae. The seasonal changes in total development time result in marked differences in the time of the diel cycle at which larvae reach first-feeding status; these differences could have more influence on survival of small larvae than effects related to either predation or food availability.

Seasonal differences in egg size, incubation, and posthatch embryonic development time have been reported for many species of temperate or higher latitude fishes. Some reports, e.g., Blaxter and Hempel (1963), involve differences between stocks or populations with different spawning seasons. Other examples, e.g., Ware (1977), deal with differences occurring over the spawning season of an apparent single stock. Hypotheses presented about the potential mechanisms or adaptive significance of seasonal differences are related to the rather marked seasonal changes in temperature, productivity, etc., that are typical of high latitude environments. Seasonal differences in egg size and early development have not been investigated in fishes from tropical latitudes where seasonal environmental changes are less extreme than at higher latitudes.

The Hawaiian anchovy or nehu, *Encrasicholina purpurea*, spawns throughout the year in enclosed, semiestuarine areas of Hawaii (Tester, 1955; Clarke 1987). Preliminary studies indicated that spawning occurs over a very short period after dusk. Because of this, it was possible not only to obtain freshly spawned eggs readily, but also to identify "day-classes" of eggs and prefeeding larvae throughout the diel cycle and thus to estimate incubation and development times from field samples. This paper reports on seasonal differences in spawning, egg size and development and considers hypotheses based on studies from higher latitudes in the context of seasonal environmental changes in the tropics.

MATERIALS AND METHODS

All material was collected from Kaneohe Bay, a semienclosed basin on the northeast side of the island of Oahu, HI. Plankton samples were collected with a 1 m diameter, 5 m long conical plankton net of 0.335 mm mesh. The net was rigged with a three-point bridle to which a ca. 3 kg weight was attached. The net was simply dropped mouth downward, allowed to fish to the bottom (12–15 m), and retrieved by a tether attached to a choke line about 1 m behind the mouth. The sample was immediatly preserved in a ca. 4% formaldehyde/seawater solution. The present study was conducted during the course of a long-term survey of nehu egg abundance that sampled stations throughout Kaneohe Bay between the hours of 0600 and 1100 at approximately weekly intervals. These samples provided eggs and larvae from the morning hours and also indicated periods and locations of high egg or larval abundance for sampling at other times of the day.

Previous studies (Clarke 1987) on adult female nehu indicated that spawning occurs during a short period (a few hours) after sunset. In order to determine spawning time more precisely, plankton samples were taken at hourly intervals between sunset and midnight at four different times of the year. Based on data from the most

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recent regular egg survey, one to three stations were sampled close to the solstices and equinoxes: 30 September 1984; 27 December 1984; 21 March 1985; and 26 June 1985. The hours sampled also included expected hatching time for the previous night's eggs for all dates except March, in which case samples were also taken at 0300–0430. The stations were also sampled in the afternoon, 1–2 days after the sunset to midnight series. Times of sunset and sunrise for the above dates were taken from astronomical tables. Water temperatures for each period were taken from the data log at the Hawaii Institute of Marine Biology laboratory at Coconut Island. Hourly surface temperatures for a 2 wk period bracketing the sampling were averaged.

Nehu eggs and larvae are easily identified. Eggs were usually very numerous (100's per sample) and were either all at very nearly the same stage or, for certain times of the day in December and March, readily separated into two age groups: eggs from the most recent spawning and much more developed eggs from the previous night's spawning. There were many fewer larvae in the samples (typically 10's per sample); in several cases larvae from 2 to 4 different samples taken within an hour of each other were combined in order to assess development at a given time of day. Larvae less than 4 mm notochord length could be separated into either two or three age groups based primarily upon presence or absence of yolk, pectoral fins and rays, and eye pigmentation. Between appearance of the pectoral fin buds and development of pectoral rays, age groups could be further discriminated using the diameter of the roughly semicircular pectoral fin bases relative to that of the pupil or the orbit (neither of which appeared to increase significantly after the pectoral buds appear). Other characters such as the development of the mouth or the gut were correlated with the principal characters used, but were not as useful for qualitative separation. For any given time of day, the least developed larvae were considered "0" group larvae (0–24 h past hatching); the next most developed, "1" group (24–48 h past hatching); and the third, if present, "2" group (48–72 h past hatching).

Except for the late afternoon samples from June, there was no difficulty in separating small larvae into age/development groups, i.e., larvae in each of the two or three groups present were similar to each other and there were no intermediates. In the June series, the apparent oldest group of afternoon larvae showed a broader range of several features than was evident for similar stages at other seasons. There was, however, still no overlap with younger stages, and after examination of more larvae from other afternoon samples taken at the same time of the year in 1984 and 1985, it was concluded that these larvae represented only one variably developed age group (see Results section). Larvae larger than 4 mm notochord length were taken infrequently, and it was not possible to estimate age groups among these on the basis of either size of development.

Volumes and dry weights were determined for undamaged newly spawned eggs from each season. Nehu eggs are ellipsoidal with the major axis about twice the minor. The yolk mass is similarly shaped and separated from the chorion by an obvious pervitelline space. For 40–50 freshly spawned eggs from each season (except June when only 29 eggs with no visible embryo were available), the major and minor diameters of both the entire egg and the yolk within were measured to the nearest 0.01 mm using an ocular micrometer at 100× magnification. Egg and yolk volumes were calculated using the formula for a prolate spheroid. Replicate samples (3 per season) of 20 eggs each were rinsed with distilled water, placed in a preweighed aluminum pan and dried at 60°C. Weights of empty and full pans were determined to the nearest 0.002 mg; weight per egg was calculated by subtraction and division by the number of eggs in the sample.

Dry weights were also determined for samples of 10–20 hydrated ovarian ova from spawning nehu taken by purse seine. Preliminary studies indicated that unless ova had already ovulated, they could not be reliably and completely separated from follicular tissue. The time between ovulation and spawning is apparently very short (Clarke 1987), and few samples of adult nehu contained many fish in this condition. Consequently, the only data reported here were from 10 females taken from a purse seine collection on 1 June 1983. This collection contained the widest size range (39–61 mm SL) of females with ova free in the oviducts.

Notochord lengths of larvae were measured to the nearest 0.1 mm. There were, however, usually less than 10 larvae of each day class at each different time of day, and statistical comparisons of average length between seasons for the same stages were not possible. The numbers of undamaged larvae suitable for dry weight determinations were even lower. Dry weight determinations were made for only three samples

of 5–10 larvae each from September and six samples of 10 each from March.

RESULTS

Spawning

The dusk-to-midnight samples from all four seasons clearly indicated that spawning was concentrated within a ca. 1 h period shortly after sunset. Newly spawned eggs, with no evidence of embryonic development under low magnification, were absent from initial samples and appeared in large numbers in samples 1.5–3 hours after sunset. The eggs in samples taken ca. 1 hour after first appearance of new eggs were already either mostly or totally in early cleavage stages. In the June series, many of the new eggs in the first sample containing new eggs were already in early cleaveage stages. Newly spawned eggs were very rare in samples taken ca. 1 hour after first appearance and were absent from later samples. Thus spawning appears to be concentrated within a period of 1 hour or less. The estimated midpoints of spawning time (Table 1) indicate that spawning occurs about 3 hours earlier in winter than in summer. The difference is not entirely accounted for by the earlier sunset in the winter months; the delay after sunset is less than in summer. These estimates of seasonal changes in spawning time agree with trends evident from mature females (Clarke 1987).

Incubation

In June and September, the incubation period was less than a day, and two day classes of eggs never occurred in the same sample. By early morning, embryos already extended about halfway around the remaining yolk. By late afternoon they extended over three-fourths of the way around the yolk, and the tail had flexed sideways. In both months the eggs apparently hatched about 22 hours after spawning time. During a 1 h period the "old " eggs disappeared, and newly hatched larvae appeared.

Incubation time was considerably longer in December and March. Eggs taken in the morning and afternoon were noticeably less developed than those from the same times in June or September. Both "old" eggs and recently spawned eggs were present between spawning time and midnight in December. No "old" eggs were present in any morning samples, and the embryos in the latest (2400 h) night samples appeared almost ready to hatch, judged from comparable stages in the June and September samples. Thus

TABLE 1.—Summary of data on spawning time, duration of egg and prefeeding larval stages, and egg size of the Hawaiian anchovy, *Encrasicholina purpurea*, in September and December 1984 and March and June 1985. Times of sunrise, sunset, spawning, and hatching are Hawaiian Standard Time. Temperature values are the means and ranges of hourly surface temperatures for a 2 wk period bracketing the sampling dates (see text). Values for egg and yolk volume are means and standard deviations of volumes calculated from length and width measurements.

	Sept.	Dec.	Mar.	June
Sunset	1800	1730	1800	1900
Sunrise	0600	0645	0600	0515
Spawning	2100	1900	2000	2200
Hatching	1900	0100	0700	2000
Temp. (°C) (range)	27.7 (27.4-28.1)	23.1 (22.5-23.9)	22.2 (21.6-23.1)	26.5 (25.9-27.1)
Incubation (h)	22	30	35	22
Hatch-feeding (h)	35	54	71	47-57
Total (h)	57	84	106	69-79
Egg weight (g)	14.8	17.9	19.5	14.9
Egg vol. (mm^3) (SD)	0.195 (0.023)	0.248 (0.024)	0.262 (0.019)	0.211 (0.016)
Yolk vol. (mm^3) (SD)	0.168 (0.020)	0.204 (0.025)	0.222 (0.022)	0.166 (0.017)

hatching time was probably about 0100 and total incubation time about 30 hours. In March, old eggs were present along with new eggs between spawning time and 0430, but were absent from the earliest postsunrise sample taken at 0820. Old eggs were, however, present in samples taken at 0600–0700 earlier in March; this indicates that hatching time was probably about 0700 and that incubation time was about 35 hours.

Early Development

Development to first feeding status was most rapid in September (Table 2). By the end of the first day, the yolk sac had disappeared, and the pectoral fin bases were almost the same diameter as the eye. By the morning of the second day, the "1" larvae had black eyes and pectoral fins with well-developed rays; most individuals had food items in the gut. Similar larvae occurred in samples taken nearer to sunrise on other dates in September–October. Thus it is likely that the "1" larvae were ready to feed at or near sunrise and that development time from hatching to first feeding was about 35 hours (Table 1).

Development was considerably slower in December and March (Table 2). Some yolk remained at the end of the first day in both months. In December, "2" larvae had already been feeding by 0800 and probably reached feeding status at or near sunrise or about 54 hours after hatching. In March, early "3" larvae taken at 0845 had already been feeding, and the late "2" larvae appeared to have reached feeding status at or just before sunrise, about 71 hours after hatching.

In June the larvae developed almost as fast during the first day as in September (Table 2), but little change took place over the second night. In the morning only a few of the "1" larvae had traces of eye pigment. By afternoon there was a relatively wide range of development among apparent "1" larvae; they had white to brown eyes and variably developed pectoral rays. The mouths of some individuals appeared

TABLE 2.—Developmental characters of different age groups of early larvae of the Hawaiian anchovy, *Encrasicholina purpurea*, at different times of the day for four different sampling dates. Codes for yolk sac (Y) are: + = present along ventral margin, T = traces anteriorly, 0 = absent; for pectoral fin; 0 = absent, B = buds visible, P = diameter of bases about equal to that of eye pupil, E = bases diameter about equal to that of eye, and R = fin rays visible; for eye pigment (E): 0 = none, T = trace, Br = brownish, Bl = black, fully pigmented. Very early stages, which would otherwise be coded "+-0-0", are coded as "NH" or "STR" depending upon whether the larvae were newly hatched and still bent anteriorly or had straightened, respectively. Larvae apparently developed to feeding status, which would otherwise be coded "O-R-Bl", are simply designated by "F".

Date / Time	Age group: Character:	"0" Y–P–E	"1" Y–P–E	"2" Y–P–E
September 1984				
1900		NH	O-E-O	
2200-2300		STR	O-E-T	
1030		T-B-O	F	
1600		O-P-O	F	
December 1984				
0800		NH	T-P-O	F
1830		STR	O-E-O	F
2330		T-O-O	O-E-T	F
March 1985				
0830		NH	T-B-O	O-E-T
1500		STR	O-P-O	O-E-?
2030-2330		+–O–W	O–E–O	O–E–Br/Bl
0330–0430		+–B–O	O–E–T	O–R–Bl
June 1985				
2100–2200		NH	O–B–O	F
0800–0900		T–B–O	O–E–O/T	F
1400–1800		O–P–O	O–R–O/Br	F

nearly fully developed. In the night samples, all early "2" larvae appeared developed to feeding stage and some had traces of food in the gut; "2" larvae in morning samples were feeding. Thus some of the June larvae may have reached feeding status just before sunset or ca. 47 hours since hatching, but many apparently did not develop to this point until after dark and did not start feeding until the next morning or about 57 hours since hatching (Table 1).

Egg Size

Dry weight and volume estimates indicated that egg size was about the same in September and June, but ca. 25% and 30% larger in December and March, respectively (Table 1). The ratios (Sept.:Dec.:Mar.:June) of estimated dry weight per egg were 1:1:21:1.32:1.01. Similar ratios for average yolk volume (1:1.21:1.32:0.99) were closer to those for weights than were the ratios for whole egg volume (1:1.27:1.34:1.08). Yolk volume averaged 79–86% of whole egg volume with no evidence of a trend with egg size. The ratios of egg to yolk for both width and length ranged between 1.05 and 1.09. Except for a value of 2.07 for March yolk length to width ratio, the other length to width ratios for both egg and yolk ranged from 2.16 to 2.26.

Available data on larval size are few, but indicate a positive relationship with egg size. In all months, the newly hatched larvae were about the same length (2.0–2.2 mm), but larvae at or near first feeding status were 3.0–3.7 mm long in March and December as opposed to 2.8–3.0 mm in September and 3.0–3.5 mm in June. Mean dry weights of late "0" and early "1" larvae from September and March were 63% and 65%, respectively, of mean egg weights for the same periods, indicating commensurately heavier larvae from the larger March eggs.

The average weight per egg of hydrated ova taken from 10 females 39–61 mm standard length was 17.8 μg. The estimates from different individuals ranged between 14.4 and 19.2 μg/egg. The value for the smallest female was well below that of the other nine (42.5–61 mm SL); the next lowest value was 16.3 μg/egg. There was, however, no correlation between average weight per egg and female length for the whole series ($P > 0.20$, Spearman rank correlation coefficient).

Discussion

The observed seasonal differences in nehu reproductive parameters are not likely owing to genetic differences between seasonal subpopulations. Nehu reach spawning size at an age of 3–4 months and rarely live as long as six months (Struhsaker and Uchiyama 1976). Thus the progeny of, e.g., March spawners would be spawning in July–September rather than the following March. Although annual changes in environmental factors in Hawaii are fewer than at higher latitudes, nehu spawn throughout the entire year rather than over a short season, and the observed differences in spawning time, egg size, etc., are most likely responses to changes in temperature, day length, light levels, etc., encountered over the entire annual cycle.

The movement of adult nehu to spawning areas and their near synchronous release of eggs are probably stimulated by decreasing light levels in the afternoon and evening, but the timing is not simply related to seasonal changes in day length and time of sunset. The delay between sunset and spawning was less in the winter, possibly because light levels in the water column decrease earlier, relative to sunset, in the winter than in the summer owing to differences in solar elevation. It is also possible that responses to light are modified by some other seasonal factor, e.g., temperature.

Seasonal changes in egg size have been reported from apparently the same stock for many other species of fishes. For example, Ware's (1977) data on egg diameters of *Scomber scombrus* in the Gulf of St. Lawrence indicate that egg volume at the beginning of the spawning season (early June) is about twice that at the end (mid-August). The central population of the northern anchovy, *Engraulis mordax*, is more similar to nehu in that it spawns year round, and maximum egg volume, which occurs in March, is about 20% greater than the minimum in September–October (Hunter and Leong 1981).

Several mechanisms for within-stock, seasonal changes in egg size have been suggested. Egg size may be related to size of the spawning females, and the seasonal trend in egg size due to the larger females' spawning early in the season and the smaller ones later (Bagenal 1971). The data on ovarian egg weights from spawning nehu indicate no relation between egg size and female size; furthermore, there is no evidence of seasonal changes in size composition of spawning nehu. Clarke (1987) found no difference in size composition between winter and summer spawners examined for fecundity; unpublished data from that study show that size composition of

spawning nehu fluctuates throughout the year, but that there is no tendency for e.g., March spawners to be larger (or smaller) than September spawners. Egg size has been shown to be both positively and negatively affected by food supply or ration (Bagenal 1969; Hislop et al. 1978). The abundance of macrozooplankton, upon which adult nehu feed, does not appear to change systematically with season in Kaneohe Bay (Hirota and Szyper 1976). Daily ration or the fraction available for reproduction could, however, change seasonally due to differences in temperature or day length, but relevant studies to consider this possibility have not been done.

Imai and Tanaka (1987) demonstrated that egg size of *Engraulis japonica* responds more directly to temperature changes, and several potential mechanisms have been proposed. Daoulas and Economou (1986) suggested that egg size would be inversely correlated with temperature if oocyte differentiation rates increased relative to oocyte growth rates with increasing temperature. Tanasichuk and Ware (1987) hypothesized that gonadotropin secretion rates increase with temperature and cause a decrease in preovulatory atresia. For a given effort per batch, this would result in more, but smaller eggs at ovulation. Nehu fecundity is higher in the summer when egg size is lowest, and the increase in the summer is only partly accounted for by higher effort per batch (Clarke 1987). If effort per batch is controlled by some other factor, either of the above hypotheses could apply to nehu.

Several studies have hypothesized that both within- and between-stock differences in egg size are adaptive and related to minimizing mortality owing to starvation of early larvae. Blaxter and Hempel (1963) showed that larvae from large herring eggs were probably better able to survive situations with low food abundance. Ware (1977) showed that egg size in *Scomber scombrus* was positively correlated with the size of food items available for newly hatched larvae. There is, however, no evidence that nehu larvae encounter marked seasonal changes in food abundance or size. Kaneohe Bay is highly productive all year; Hirota and Szyper (1976) found no seasonal trends in total microzooplankton abundance. My own unpublished data indicate that concentrations and sizes of small copepod nauplii, the dominant prey of first-feeding nehu larvae (Burdick 1969), are similar throughout the year.

Ware (1975) and Tanasichuk and Ware (1987) have shown that a mechanism resulting in a decrease in egg size with increasing temperature would be selectively advantageous if egg and larval mortality rates were inversely related to egg size and if incubation times were inversely related to temperature (and not to egg size). Small nehu eggs and larvae would probably be subject to higher mortality owing to predation than would larger eggs and larvae at all times of the year, regardless of the apparent lack of variability in larval food supply. Furthermore, Yamashita's (1951) results indicate that differences in incubation time are caused by temperature and not egg size. Yamashita incubated nehu eggs from a single sample from Kaneohe Bay at different temperatures. Allowing for the fact that all his eggs had already spent a few hours at ambient temperature, the change in incubation time with temperature was similar to that evident from the seasonal data of the present study. Similar studies on other engraulids (King et al. 1978; Lasker 1964) have also shown negative correlations between incubation time and temperature that were presumably independent of egg size. Thus Ware's (1975) basic assumptions and hypothesis about factors selecting for egg size-temperature relationships seem to be applicable to nehu.

The duration of the period between hatching and first feeding (HF) was also negatively correlated with temperature. There were, however, seasonal differences in the ratio of posthatch to prehatch embryonic development time. HF was 1.60, 1.78, 2.02, and 2.14 times incubation time for September, December, March, and June, respectively (using HF = 47 hours for June). This indicates either that the effects of temperature on HF are qualitatively different from those on incubation, or that some other factor also affects posthatch development rate. For a range of temperatures that included those observed in this study, Houde (1974) showed that increasing temperature caused decreases in the period between hatching and eye pigmentation of larval *Anchoa mitchelli*. To the extent that seasonal differences in HF of nehu are similarly caused by temperature differences, this would tend to augment any selective advantage for larger eggs and larvae during the winter.

Even though Ware's (1975) hypothesis could potentially apply to nehu, the point in the diel cycle at which larval feeding becomes possible could have more important consequences to larval survival than differences in either egg size or

total development time. Small nehu larvae feed only during the day (Burdick 1969; Johnson 1982). In September, December, and March, larvae reached first-feeding status at or shortly before sunrise, could begin feeding as soon as they were able, and had an entire day to feed before having to survive the next night. In June, however, the larvae reached first-feeding status near sunset, had little or no chance to feed, and had to survive the night mostly or solely on internal reserves. Nehu larvae would face situations similar to June whenever the total time from spawning to first-feeding status was close to a multiple of 24 hours. (Other such periods would have occurred between September and December, between December and March, and between March and June.) If larvae during such periods had exhausted their internal reserves before they had a chance to feed, survivorship could have been greatly reduced compared with periods when larvae reached first-feeding status near dawn.

The time between reaching first-feeding status and irreversible starvation of nehu larvae is not known. It is usually of the order of days for fishes from higher latitudes (Hunter 1981), but is probably considerably less for nehu given that their incubation and development times are much shorter than those of most higher latitude species. Houde (1974) found that survival and growth of larvae of *Anchoa mitchelli* at 22°–28°C was unaffected by delaying feeding up to 24 hours or more after development of eye pigmentation, but nehu may be less tolerant. The development time between hatching and feeding status is longer for nehu than for *A. mitchelli* at similar temperatures, and visible yolk is gone at an earlier stage in nehu.

The seasonal changes in total time between spawning and reaching first-feeding status thus could result in fluctuations of mortality rates of nehu larvae throughout the year independent of either food supply or predation rates. Such fluctuations would not be expected in species from higher latitudes because differences of a few hours between reaching first-feeding status and the opportunity to feed are probably not as critical. Furthermore, spawning in many species, e.g., the northern anchovy, *Engraulis mordax*, is not as synchronous as in nehu and is spread over a broader portion of the diel cycle (Hunter and Macewicz 1980). Consequently, larvae from a given day's cohort would reach first-feeding status at various points during the diel cycle regardless of the absolute duration of the period between spawning and HF status.

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Larval Production and Mortality of Pacific Saury, *Cololabis saira*, in the Northwestern Pacific Ocean[1]

Yoshiro Watanabe and Nancy C. H. Lo

ABSTRACT: Because quantitative samples of saury eggs are difficult to obtain owing to their adhesive nature, reproductive level of the Pacific saury, *Cololabis saira*, has been estimated from the standing stock of the larvae and juveniles in Japan. Mortality curves were constructed and daily larval production at hatching was estimated for combined data from 1972 to 1986 and for consecutive individual years within this period. Durations of size classes were estimated from a growth curve and used to calculate fish production at age. Because number of fish captured by a net tow (area = 401.3 m^2) showed a diel cycle due to fish behaviors, such as net frame evasion and diel vertical movement, the average mortality curve for 15 years was based on data collected at night. We used an exponential decay model to describe the mortality of saury larvae and juveniles. The daily instantaneous mortality rate was 0.078, and the larval production at hatching was 1.255 larva/tow/day. Mortality curves for the individual years were based on data collected throughout the day and night after correction by size- and time-specific retention rates. Daily larval production at hatching fluctuated among individual years ranging from 0.154 to 5.176. Daily instantaneous mortality rates positively correlated with larval production at hatching, which might indicate the presence of a density-dependent process in larval mortality.

Together with the Japanese sardine, *Sardinops melanosticta*, and the mackerels, *Scomber japonicus* and *S. australasicus*, the Pacific saury, *Cololabis saira* (Brevoort), is one of the most important offshore pelagic fishes in Japan. Although total catch of the saury in Japan (210,000 t [metric tons] in 1984) was much smaller than that of the sardine (4,180,000 t) or the mackerels (810,000 t) (Statistics and Information Department, Japan 1986), more than 95% of the catch is destined for human consumption (Japan Saury Fishery Association 1985). In sharp contrast, the sardine (81%) and the mackerel (40%) catches (Fisheries Agency 1985) are procesed for animal foods.

Saury fishermen in Japan expect to have a reliable fishing forecast provided by the Tohoku Regional Fisheries Research Laboratory, Fisheries Agency of Japan, every summer before the beginning of the fishing season. The forecast includes the expected catch in the coming season and the potential fishing grounds. The expected catch depends on fish stock size, and the location and size of the fishing grounds are a function of fish migration in relation to oceanographic conditions. Fish stock size is determined by both reproductive level and mortality rates of developmental stages from postspawning through recruitment. Since the saury grows rapidly and becomes an adult within one year (Watanabe et al. 1988), larval production and mortality rate in young stages are believed to be more or less directly related to recruitment and catchable stock size. Matsumiya and Tanaka (1978) suggested from their intensive study of population dynamics of the northwestern Pacific saury that the fluctuations of population size are seriously affected by reproductive success.

An egg survey may be the best method for estimating the reproduction level of pelagic fishes. However, it is difficult to conduct a quantitative egg survey of the saury by towing plankton nets because the eggs attach by filaments to floating objects such as drifting kelp. We therefore have been conducting larval and juvenile surveys to estimate the reproductive level. We use catch/tow (number of fish/net tow) values of several size classes as abundance indices. The year-to-year changes of the indices may reflect the fluctuation of reproductive level.

The apparent number of larvae in a size class is influenced by the duration of growth through that size class. If growth is slow, the duration will be extended; conversely, if growth is fast, the duration will be short. The duration of growth through a size class thus defines the

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amount of time that larvae or juveniles are vulnerable to capture. Because the growth rate is not constant over the size range of the young fish sampled in this study, we must correct for this bias. The production of larvae by age is defined as the abundance of larvae by size divided by the duration of growth through the size class, which is expressed as catch/tow/day. This allows us to calculate instantaneous mortality rate (IMR), and thus, construct a mortality curve. We need to know age and growth rate of saury to calculate production at age and mortality rates.

In northern anchovy, *Engraulis mordax*, there have been extensive studies of eggs and larvae, and the methods to calculate the production and mortality rate were established (Zweifel and Smith 1981; Lasker 1985; Lo 1985; 1986). Ichthyoplankton survey data, embryonic incubation times, and larval growth rates are the essential parameters for this method. Further, one needs to have information on possible biases of tow data. For the Pacific saury, we have 15 years of larval net-tow data, a newly developed growth model based upon otolith growth increments (Watanabe et al. 1988), and information on bias correction of tow data for day and night differences. All these make it possible to compute fish production at different ages and mortalities. Extending the mortality curve to age 0, we can calculate larval production at hatching, which might be the best index of reproductive level so far available. In this paper we selected the exponential decay mortality curve and used it to calculate the larval production at hatching and the daily IMR of Pacific saury in the northwestern Pacific Ocean for 1972–86.

METHODS

Data Source

The Pacific saury spawns nearly all year round in the entire northwestern Pacific Ocean. The sampling areas and seasons were somewhat different from year-to-year, but our data set of 15 years (1972–86) included around-the-clock samples taken all year from a large area of the northwestern Pacific, lat. 29–45°N, long. 129–174°E (Fig. 1).

Saury larvae and juveniles were collected by a surface ring net that was towed for 5 minutes at 2 knots. The mouth diameter was 1.3 m, and therefore the surface area covered by one tow was 401.3 m^2. A mesh size of the 3.0 m forward part of the net was 2.0 mm, and the 1.5 m rear part was 0.33 mm. Samples were washed down after the 5 min tow and preserved in 10% unbuffered formalin. Larvae and juveniles of saury were measured to the nearest 0.1 mm knob length (KnL), the distance from the tip of the lower jaw to the posterior end of a muscular knob at the base of the caudal peduncle. They were then grouped into 11 size classes from 7.5 mm (including 5.0–9.9 mm) up to 57.5 mm (55.0–59.9 mm). The midpoint and both limits of each class were then converted into the capture size before preservation, using a shrinkage factor by formalin preservation (0.97) reported by Theilacker (1980) for northern anchovy. The midpoint of each size class was used to represent the class, though it is not a mean age of the class. The capture size was converted to age, and duration of each size class was obtained using the growth model developed by Watanabe et al. (1988). The growth equation from hatching to a 100 mm juvenule is

$$\mathrm{KnL} = 5.90 \exp((0.0865/0.0293) \times (1 - \exp(-0.0293\, t)))$$

where KnL is the fish knob length in mm after capture (before preservation) and t is the age in days from hatching.

Bias Corrections

An ichthyoplankton survey is essential for most pelagic fish research (Smith and Richardson 1977), but it is not bias free. The most common biases in catch of fish eggs and larvae are extrusion of eggs and larvae through net mesh and evasion of a net frame by fish. For the Pacific saury, the mesh size of the anterior part of the net, 2.0 mm, might be large enough to lose larvae by extrusion. Vulnerability of the fish to a net tow varies throughout a day due to changes in evasion abilities. Availability of the fish to a tow changes as well due to diel vertical movement. These factors result in differences in numbers of fish captured by net tows during the day and night. For the analysis, we defined 10 diel time periods based upon angles between the center of the sun and the celestial horizon. We used four periods in the morning—DAWN (DWN), MORNING TWILIGHT (MTW), SUNRISE (SRS), and MORNING (MRN)—and another four periods in the evening—AFTERNOON (AFT), SUNSET (SST), EVENING TWILIGHT (ETW), and DUSK (DSK). Time dura-

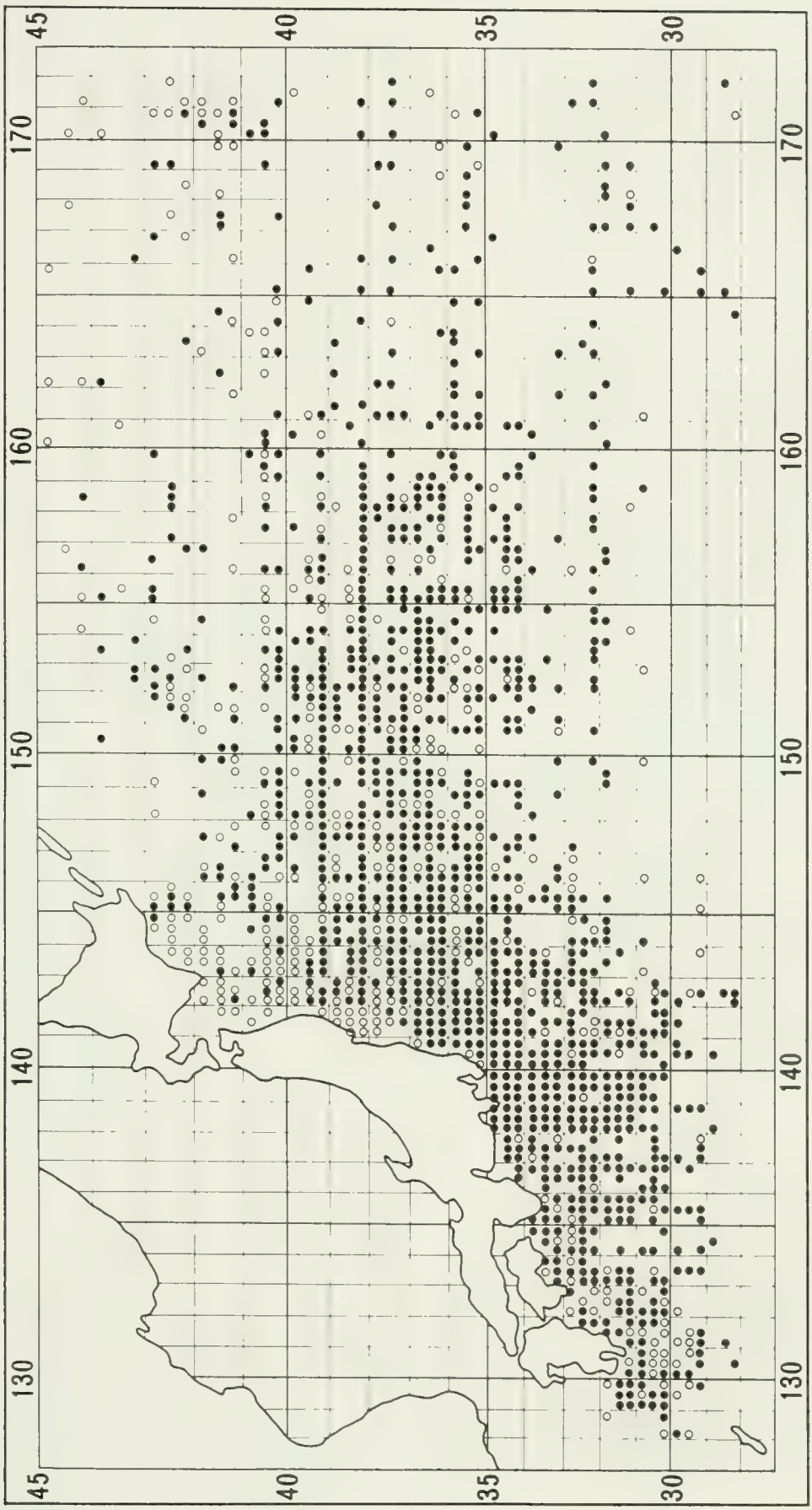

FIGURE 1.—Composite survey area of Pacific saury larvae and juveniles in the northwestern Pacific Ocean, 1972–86. Solid (open) circles represent areas where a positive tow has ever (never) been recorded in the period.

tion between the end of MRN and the beginning of AFT was named DAYTIME (DAY), and the time duration between the end of DSK and the beginning of DWN was named NIGHTTIME (NIT). We examined the data collection of 15 years (1972–86) and estimated size- and time-specific retention rates. Changes of these values are due to the fish behaviors such as net frame evasion and vertical migration. The rates were calculated by taking ratios of catch/tow in each time category and that of the NIT (Table 1). Extrusion of larvae was examined as well, comparing observed numbers of fish with predicted numbers calculated from a mortality curve (see results section for detail).

To reduce the seasonal effect of larval production and mortality, we also considered the bias on average catch/tow within a year from unproportional sampling efforts among months. Net tows were concentrated between February and May; the percentage of juvenile fish in the total catch was low in winter and increased in spring and early summer (Fig. 2). Thus, we divided 12 months of the year into 4 seasons based upon the abundance of saury larvae and juveniles: January to March as the main spawning season, April to June as the late spawning season, July and August as the off spawning season, and Sep-

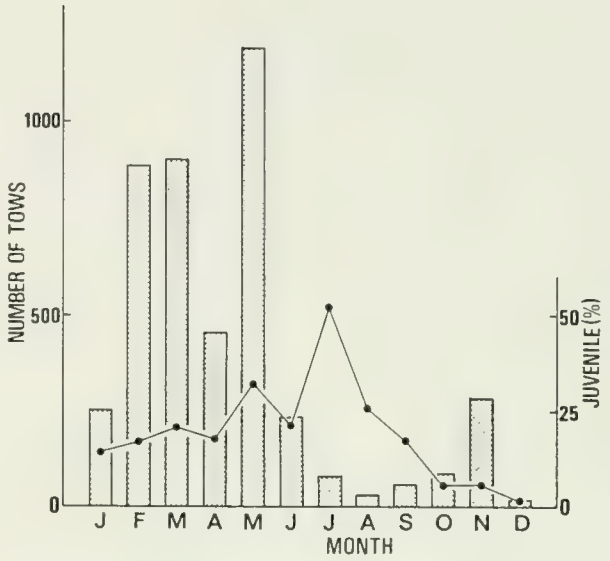

FIGURE 2.—Number of tows (columns) and percentage of juvenile Pacific sauries (dots) in total fish captured by months.

TABLE 1.—Annual average of Pacific saury catch/tow (c/t) and size- and time-specific correction factors (CF) of size classes in 10 time categories.

Size class (mm):		7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5
Time category (# tows)												
SRS	c/t	1.115	1.495	0.330	0.065	0.260	0.021	0.011	0.005	0.026	0.021	0.058
(92)	CF	0.864	0.724	0.220	0.072	0.475	0.064	0.050	0.029	0.215	0.158	0.450
MRN	c/t	1.588	2.281	0.521	0.352	0.154	0.043	0.039	0.028	0.019	0.003	0.000
(165)	CF	1.231	1.104	0.348	0.390	0.282	0.131	0.176	0.165	0.157	0.023	—
DAY	c/t	1.400	1.134	0.509	0.209	0.098	0.042	0.034	0.008	0.002	0.002	0.016
(1,517)	CF	1.085	0.549	0.343	0.232	0.179	0.128	0.154	0.047	0.017	0.015	0.124
AFT	c/t	2.090	2.004	1.022	0.403	0.176	0.039	0.018	0	0	0	0.003
(199)	CF	1.620	0.970	0.682	0.447	0.322	0.119	0.081	—	—	—	0.023
SST	c/t	1.486	1.175	0.937	0.501	0.524	0.189	0.006	0	0	0	0
(97)	CF	1.152	0.569	0.626	0.555	0.958	0.578	0.027	—	—	—	—
ETW	c/t	0.422	0.782	0.393	0.218	0.133	0.079	0.070	0.031	0.017	0.014	0.007
(132)	CF	0.327	0.379	0.262	0.242	0.243	0.242	0.317	0.182	0.140	0.105	0.054
DSK	c/t	1.425	1.700	1.354	0.867	0.641	0.268	0.340	0.428	0.192	0.121	0.084
(218)	CF	1.105	0.823	0.904	0.961	1.172	0.820	1.538	2.518	1.582	0.910	0.651
NIT	c/t	1.290	2.066	1.498	0.902	0.547	0.327	0.221	0.170	0.121	0.133	0.129
(1,805)	CF	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000
DWN	c/t	0.803	1.465	1.285	0.750	0.499	0.313	0.205	0.152	0.082	0.088	0.053
(203)	CF	0.622	0.709	0.858	0.831	0.912	0.957	0.928	0.894	0.678	0.662	0.411
MTW	c/t	0.568	0.610	0.434	0.250	0.158	0.053	0.026	0.046	0.020	0.092	0.020
(80)	CF	0.440	0.295	0.290	0.277	0.289	0.162	0.118	0.271	0.165	0.692	0.155

[1]SRS = SUNRISE; MRN = MORNING; DAY = DAYTIME; AFT = AFTERNOON; SST = SUNSET; ETW = EVENING TWILIGHT; DSK = DUSK; NIT = NIGHTTIME; DWN = DAWN; MTW = MORNING TWILIGHT.

tember to December as the early spawning season (Fig. 3). We calculated catch/tow values of 4 seasons separately in every size- and time-group by summing up the number of fish and net tows of 15 years and then taking average catch/tow values of 4 seasons. These values, average catch/tow values of the year, were used for calculation of the size- and time-specific retention rates mentioned above.

Mortality Models and Computations

The mortality model of the young saury from hatching (age 0) to 52 days old (57.5 mm preserved KnL) was based on the data of catch/tow/day (daily production) at ages. Two types of mortality curves were fitted to both the combined data collected in the NIT period for 1972–86 and the data set from 14 individual spawning years. One mortality curve is based on an age-dependent instantaneous mortality rate (IMR), $Z_1(t) = \beta/t$, and the other based on the age-independent constant IMR, $Z_2(t) = \alpha$, where t is the fish age in days and α and β are coefficients of IMR. The age-dependent IMR was considered because of the possibility that early larvae may suffer higher mortality than the older ones, as in the case of northern anchovy larvae along the California coast (Lo 1985, 1986). We constructed both mortality curves for saury larvae and juve-

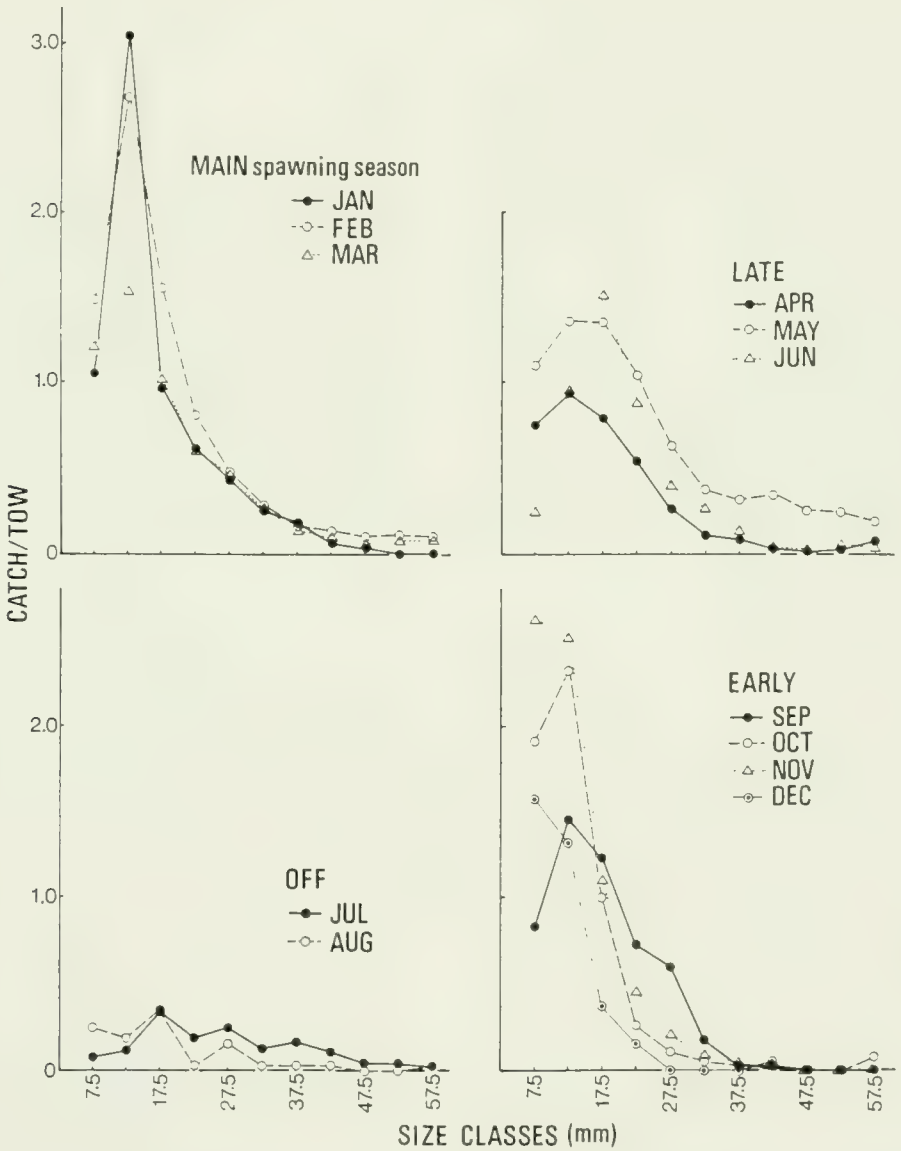

FIGURE 3.—Division of the year into four spawning seasons based on the number of Pacific sauries captured by a net tow (catch/tow) by months.

niles. The mortality curves based on $Z_2(t)$ fitted the larval and juvenile data better than $Z_1(t)$, and therefore, we chose $Z_2(t)$ to describe the fate of young sauries. The mortality curve with a constant IMR takes the form of the exponential mortality curve,

$$P_t = P_0 \exp(-\alpha t)$$

where P_t is the daily fish production at age t, t is the age in days from hatching, P_0 is the daily larval production at hatching, and α is the daily IMR.

For the computation of larval production and mortality rate averages of 15 years, we used the data of the NIT category. For the computations of individual years, however, the number of NIT samples were not sufficient; therefore, we had to use the data from all the time periods. The data sets of individual years were classified into 10 time periods of 11 size classes and were corrected by dividing numbers of fish by their specific retention rates (Table 1). The corrected numbers of fish were summed up in each size class and divided by the total number of tows of the year to calculate catch/tow values as the abundance index of each size class.

We used the catch data of the early, main, late, and off spawning seasons (from September to August of the following year) as a unit of a spawning year instead of the calendar year. According to the recent growth model by Watanabe et al. (1988), the saury becomes adult within a year, so, we supposed that the larvae produced in a spawning year constitute the major part of the year class of the current year.

The catch/tow value of each size class was further divided by the duration of the corresponding size class. This provided the production rate (catch/tow/day), which was used for the computation of larval production at hatching and mortality. The parameters, larval production at hatching (P_0) and daily IMR, are estimated by using a nonlinear program (Par (Dixon et al. 1985)).

RESULTS

The Overall Mortality Curve for 1972–86

To understand the fate of young sauries from 1972 to 1986, the average catch/tow/day from the NIT samples (Table 2) was used to estimate the larval production at hatching and the IMR. All the fish were first grouped into 11 size classes, ranging from 7.5 mm (5.0–9.9 mm) to 57.5 mm (55.0–59.9 mm), and the midpoint of each size classes was converted to age. The data from the first two size classes (7.5 mm and 12.5 mm) were excluded from the analysis because the catch/tow/day in these two size classes was lower than the next older larvae. The downward bias could be due to extrusion of the larvae through the mesh. The estimates of the larval production at hatching (P_0) and daily IMR were 1.255 larvae/tow/day (SE = 0.111) and 0.078 (SE = 0.004), respectively (Fig. 4). The total daily mortality rate ($(P_{t-1} - P_t)/P_{t-1} = 1 - (\exp(-\alpha))$) was 7.5% from the newly hatched larvae to the 52 d old juvenile.

TABLE 2.—Daily production (catch/tow/day) at age (day) of Pacific saury from NIGHTTIME samples, 1972–86.

Midpoint size (mm)	pr[1]	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5
	cp[2]	7.7	12.9	18.0	23.2	28.4	33.5	38.7	43.8	49.0	54.1	59.3
Age (day)		3.2	10.5	16.2	21.3	25.9	30.3	34.5	38.8	43.1	47.4	52.0
Size range (mm)	pr	5.0–	10.0–	15.0–	20.0–	25.0–	30.0–	35.0–	40.0–	45.0–	50.0–	55.0–
	cp	5.2–	10.3–	15.5–	20.6–	25.8–	30.9–	36.1–	41.2–	46.4–	51.5–	56.7–61.8
Stage duration (day)		7.1	6.4	5.3	4.9	4.4	4.3	4.2	4.3	4.3	4.4	4.7
# fish observed		2,030	3,982	3,352	2,148	1,333	821	536	406	330	375	351
Catch/tow		1.125	2.206	1.857	1.190	0.739	0.455	0.297	0.225	0.183	0.208	0.194
Daily fish production		[3]0.158	[3]0.345	0.350	0.243	0.168	0.106	0.071	0.052	0.043	0.047	0.041

[1]Fish knob length after preservation.
[2]Fish knob length after capture (before preservation).
[3]Not used for the computation

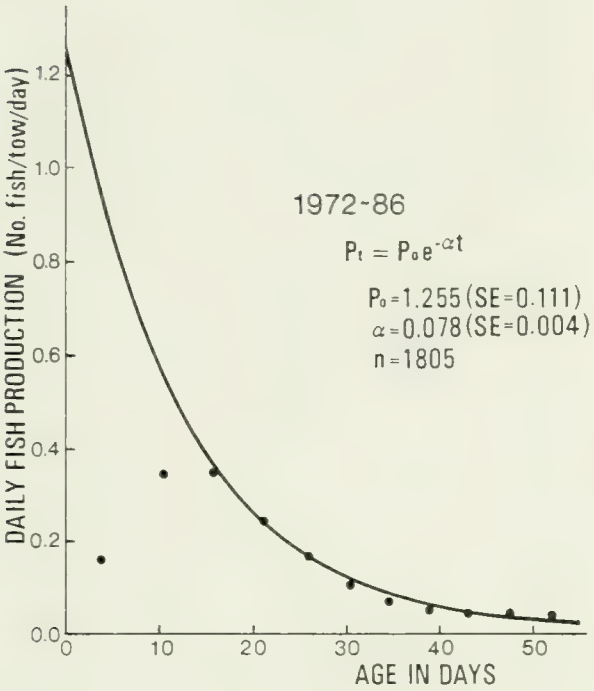

FIGURE 4.—Mortality curve of young Pacific saury calculated from fish production at ages calculated from the NIT data of 15 years (1972–86). Data points of the smallest two size classes were not used for the computation. P_0 is the larval production at hatching, α is the daily IMR, and n is the number of tow samples.

Mortality Curves for Individual Spawning Years

To assess the mortality of young saury for individual spawning years, we used all the tow data collected around the clock, after the correction of catch data by the size- and time-specific retention rates (Table 1). The correction procedures are the same for all the spawning years. To illustrate the data assemblage and computation, the 1979 catch data set for 11 size classes was given (Table 3). Again, the data points of the first two size classes were not used in the estimation procedure because of the apparent downward bias. The parameter estimates and the mortality curves are summarized in Table 4, and the mortality curves are presented in Figure 5.

The larval production at hatching (P_0) fluctuated by more than 30-fold from the maximum 5.176 larvae/tow/day in 1978 to the minimum 0.154 in 1985 spawning year. Daily IMR has also ranged from 0.115 down to 0.041, with daily mortality rates of 10.9% and 4.0%, respectively.

Year-to-year fluctuations of these two parameters (P_0 and IMR) and the total catch of saury in Japan (Statistics and Information Department, Japan 1987) are presented in Figure 6. The total catch of saury can be an index of the stock size, though possibly including effects of economic factors such as fish price. The fishing season of saury opens in the first half of August and closes in the middle of December. Since the saury becomes adult in 9–10 months and 2 yr old fish were not found in the northwestern Pacific

TABLE 3.—Daily production (catch/tow/day) at age (day) of Pacific saury in 1979 spawning year (September 1978–August 1979).

Midpoint size (mm)	pr[1]	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5
	cp[2]	7.7	12.9	18.0	23.2	28.4	33.5	38.7	43.8	49.0	54.1	59.3
Age (day)		3.2	10.5	16.2	21.3	25.9	30.3	34.5	38.8	43.1	47.4	52.0
Size range (mm)	pr	5.0–	10.0–	15.0–	20.0–	25.0–	30.0–	35.0–	40.0–	45.0–	50.0–	55.0–
	cp	5.2–	10.3–	15.5–	20.6–	25.8–	30.9–	36.1–	41.2–	46.4–	51.5–	56.7–61.8
Stage duration (day)		7.1	6.4	5.3	4.9	4.4	4.3	4.2	4.3	4.3	4.4	4.7
# fish observed		607	1,267	738	420	194	68	61	32	16	13	9
# fish corrected		674	1,470	939	625	245	98	90	62	22	14	10
Catch/tow		1.685	3.676	2.349	1.562	0.613	0.244	0.226	0.155	0.054	0.036	0.026
Daily fish production		[3]0.236	[3]0.574	0.443	0.319	0.139	0.057	0.054	0.036	0.013	0.008	0.006

[1]Fish knob length after preservation.
[2]Fish knob length after capture (before preservation).
[3]Not used for the computation.

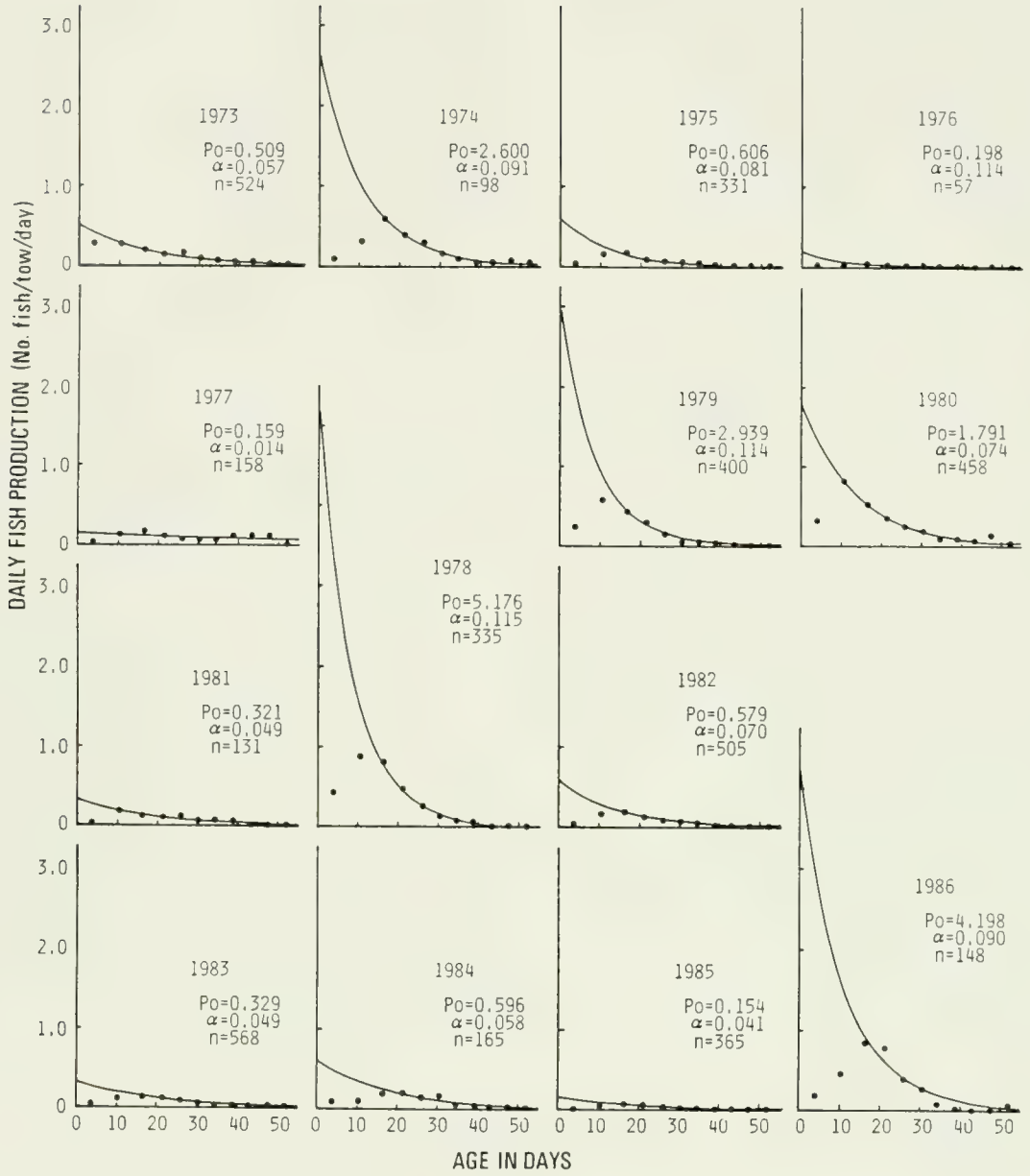

FIGURE 5.—Mortality curves of individual spawning years. P_0 is the Pacific saury larval production at hatching, α is the daily IMR, and n is the number of tow samples.

(Watanabe et al. 1988), the total catch in a fishing season must come from larvae produced in the spawning period of the same year. For example, the 1973 catch is related to larval production at hatching and daily IMR of the 1973 spawning year (from September 1972 to August 1973).

Larval production at hatching and the daily IMR have fluctuated somewhat concordantly from 1973 to 1986. The Spearman's Rho is 0.704 ($n = 14$, $P < 0.05$), indicating a positive correlation between P_0 and IMR among years. The exception to this trend was 1976. The production value of 1976 was one of the lowest in 14 years whereas the daily IMR was very high, probably resulting in a minimum catch of <100,000 t in 1976.

Mesh Retention of Larvae

The low values of larval production for the first two size classes precluded their use in the estimation of larval mortality. Since the mesh size of the anterior 3.0 m of the net is 2.0 mm, we

TABLE 4.—Daily larval production at hatching (P_0) and daily instantaneous mortality rates (IMR) of individual spawning years with standard error in parentheses.

Spawning year	P_0 (larva/tow/day)	IMR	Mean square error ($\times 10^{-4}$)
1973	0.509 (0.100)	0.057 (0.008)	4.05
1974	2.600 (0.410)	0.091 (0.007)	10.20
1975	0.606 (0.112)	0.081 (0.009)	1.37
1976	0.198 (0.080)	0.114 (0.022)	0.13
1977	0.158 (0.067)	0.014 (0.013)	19.00
1978	5.176 (0.433)	0.115 (0.004)	3.33
1979	2.939 (0.653)	0.114 (0.012)	8.02
1980	1.791 (0.284)	0.074 (0.007)	12.50
1981	0.321 (0.100)	0.049 (0.012)	6.00
1982	0.579 (0.084)	0.070 (0.006)	1.36
1983	0.329 (0.055)	0.049 (0.007)	1.83
1984	0.596 (0.213)	0.058 (0.015)	17.10
1985	0.154 (0.037)	0.041 (0.009)	1.30
1986	4.198 (1.325)	0.090 (0.015)	104.00

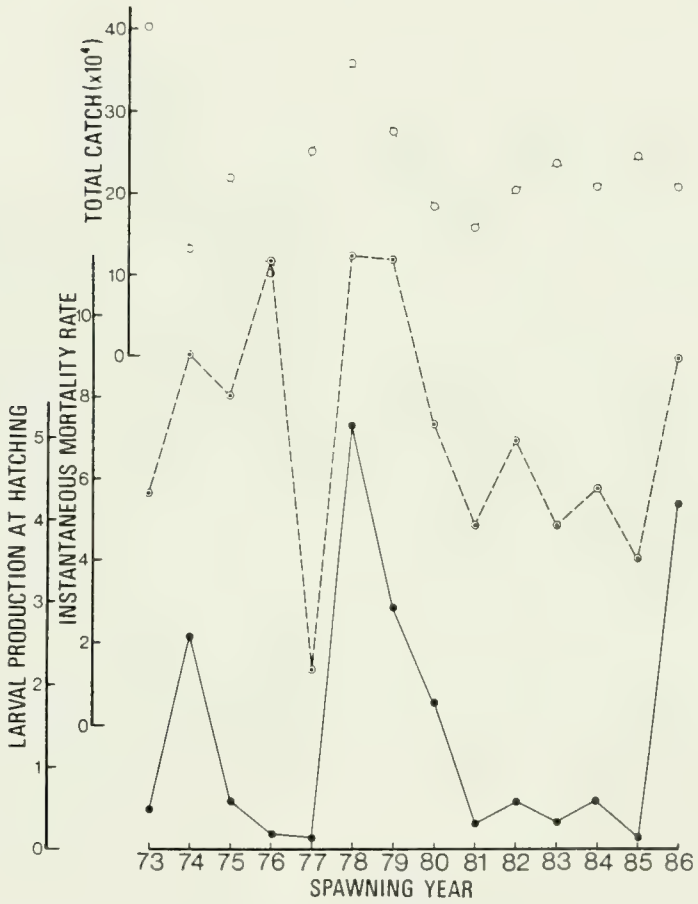

FIGURE 6.—Year-to-year fluctuations of daily Pacific Saury larval production at hatching in number of larvae per tow (———●———), daily IMR (------⊙------), and the annual total catch in metric tons (-----○-----) of the saury.

think that the downward bias is due to extrusion through the mesh. The mesh retention rate of larvae in the first two size classes could be estimated from the ratio of the observed catch/tow/day and the predicted larval production computed from the overall average mortality curve of 15 years. The estimate of mesh retention rate for larvae of 7.5 mm (3.2 days old) is,

Observed: 0.158 (larvae/tow/day)
Predicted: 0.978 (larvae/tow/day) = 1.255 exp(−0.078 × 3.2)
Retention rate: 0.16 = 0.158/0.978

and for larvae of 12.5 mm (10.5 days old) is,

Observed: 0.345 (larvae/tow/day)
Predicted: 0.553 (larvae/tow/day) = 1.255 exp(−0.078 × 10.5)
Retention rate: 0.62 = 0.345/0.553.

DISCUSSION

Production and mortality rates of fish larvae and juveniles cannot be obtained without good growth models, which are indispensable in calculating stage durations. A new growth model based on growth increments of otoliths has recently been established (Watanabe et al. 1988) enabling calculation of mortality rates. The current results are virtually the first attempt to calculate larval production at hatching. These should provide the best index of reproductive level ever obtained.

Sablin (1978) first calculated mortality rate of juvenile saury for 8 individual years (1968–75), using catch/tow values of two size groups, 26–30 mm and 46–50 mm, and 20 mm/mo as a growth rate of this size range. The average monthly IMR estimated by Sablin was 1.15 with a range from 0.76 to 1.62. He obtained the IMR from 2 size groups for individual years, whereas we used catch data from 9 size classes in computing the IMR. We believe the estimates of IMR reported here are an improvement over those of Sablin.

Monthly mortality rates using the Sablin IMRs (1978) ranged from 53.2% to 80.2% with an average of 68.3%. These values were much lower than the monthly rates calculated from the daily IMRs in this paper, 70.8–96.8% with an average 90.4%. The discrepancy between the two seems to derive from the difference in growth rates used for the computations (Fig. 7). Sablin used a rate of 20 mm/mo (0.67 mm/d) for the size range from 26–30 mm to 46–50 mm. We used the growth model by Watanabe et al. (1988), which shows that sauries grow from 27.5 mm to 47.5 mm in 17.2 days (1.16 mm/d). This was 1.7 times faster than growth rate of Sablin. We recalculated monthly mortality rates using the Sablin IMRs and the Watanabe et al. growth rate of 1.16 mm/d producing estimates close to ours, 73.4–94.1% with an average of 86.5%.

The absolute value of total annual production of newly hatched larvae of the Pacific saury can be calculated from our results using the assumptions that 1) all fish in a vertical water column are in the upper one meter, and 2) those in a volume of water strained are captured by the net during the NIT period. The values of larval production at age 0 are on daily basis over the area covered by a net tow. Thus, the annual total production of the hatched larvae can be computed as below:

$$\text{Annual Total Production of Hatched Larvae} = P_0 \cdot 365 \cdot A/401.3$$

where P_0 is larval production at hatching, A is total spawning area in m^2, and 401.3 is surface area in m^2 covered by one net tow. However, the distribution of saury larvae and juveniles in the northwestern Pacific extends far to the east of Japan, and we cannot delimit the total spawning area. Thus, calculation of the absolute larval production of saury at hatching for the entire area is not practical. However, the calculation of abso-

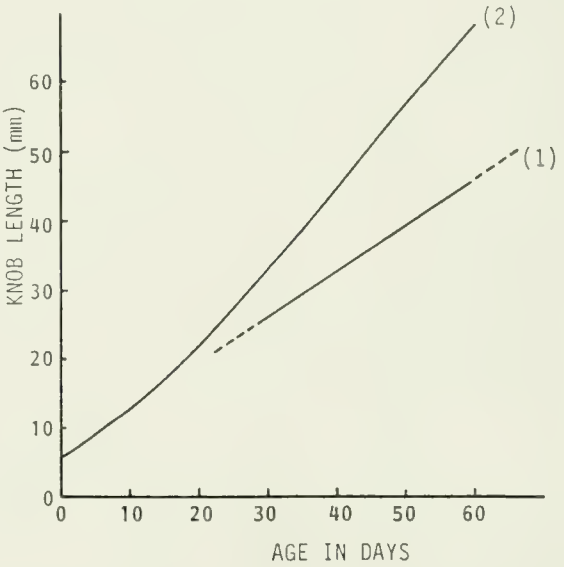

FIGURE 7.—Growth curves used by Sablin (1973) (1) and by us (2) for Pacific saury.

lute larval production in a limited area, which can be covered with a high precision, is possible and will be useful.

The assumption that all the fish in a volume of water strained by the net tow are captured in the NIT period is not realistic for a variety of reasons. The larval net used in this study has bridles in front of the mouth, and to some extent evasion can be expected due to turbulence in front of the net. Visual evasion is possible even in the NIT period because natural waters are not totally dark due to moonlight and a variety of bioluminescent organisms.

Vertical distribution pattern of young sauries has been investigated by towing nets on horizontal strata at several depths (Okiyama 1965; Parin 1967). However, the fraction of the young saury population in the upper one meter available to our net is not known.

The volume of water filtered by a tow may be different among tows depending on wave conditions, mesh clogging, etc. The standardization of catch data by a volume of water filtered must also be done to improve the accuracy of estimates. In our study, we did not have a flow meter with our net. Biases, resulted from these problems, must be resolved before absolute larval production can be obtained.

Unaccounted variances due to the retention correction factor and the duration computed from growth curve could lead to underestimation of the variance of parameter estimates in the mortality curve. On the other hand, the standard error of both P_0 and IMR in the current paper may be higher than the estimates from a regression where each daily fish production estimate is weighted by the inverse of its variance. The effect of the unaccounted variance caused by the retention correction factor could be small because the retention rates were computed from a large number of tows, reducing the standard error of estimated retention to insignificant levels. The variance of duration is unknown. Theoretically it could be estimated from the growth curve, but we did not compute it. A simulation study on evaluating the precision and bias of mortality estimates for northern anchovy (N.C.H.L., unpubl. data) indicated that the variation contributed from bias correction factors is minimal.

We employed an age-independent mortality model in this paper. This does not necessarily mean that the mortality of saury larvae is age-independent. Because of biased catch data due to mesh extrusion in the smallest two size classes, we could not use these two values. This might have had some effect on choosing a mortality model. For further studies we have devised a cylinder-conical larval net for saury that is constructed with one type of mesh (0.53 mm). The body depth at the pectoral fins in early post-yolk-sac larvae is 0.6–0.7 mm, so the new net is expected to retain larvae of the smallest size classes. Thus, the net will enable us to get an unbiased sample of early larvae, and the use of a data set of all size classes including 7.5 and 12.5 mm classes might cause a shift of the mortality model from age-independent to age-dependent type.

Because mortality is a necessary piece of information for computing mean age for each size group, we used the ages corresponding to the midpoints of the size classes for the mortality computation instead of mean ages. It is acceptable to use the midpoint to convert size to age when the mortality information is unavailable, when mortality is low, or when the size interval is small. Bias resulted from the use of the midpoint was large for the first size class: 2.4 days with mortality correction assuming the IMR = 0.08 and 3.2 days using the midpoint 7.7 mm. However, the first two size classes were not included in the mortality computation, so bias caused by using the midpoints was minimal.

The high production values in large juvenile classes (Table 2, Figs. 4, 5) may be due to an underestimation of the durations of these size classes. Year-to-year variations of growth may be large enough to cause considerable differences in durations. The standing stock of larvae in a size class is influenced by the duration of growth through that size class. Because an accurate mortality estimate depends on accurate growth rate estimates, calculation of the growth rate every year, or at least every time the fish size composition changes, is necessary to obtain accurate mortality rates for individual years.

As shown for the northern anchovy, direct estimates of spawning biomass from an ichthyoplankton survey can be obtained (Lasker 1985). This method can be applied to other fishes that produce pelagic eggs. However, the saury produces adhesive eggs and quantitative sampling of them is difficult. Larval census is so far the best index for spawning biomass of the saury. Even if it were possible to obtain quantitative samples of eggs, uncertainties in embryonic mortality rates may rule out use of egg production. The saury has a long incubation time of about 2 weeks under 13°C (Yusa 1960), and slight differ-

ences in the daily mortality rates of embryonic stages, rather than egg production, could have profound influence on larval production at hatching. In other words, larval production at hatching may not necessarily be accurately related to egg production without knowing mortality rates of embryonic stages. Although crude estimation of spawning biomass by conventional plankton tows might be possible (Smith et al. 1970), a radical departure from the egg sampling method using information on vertical and horizontal distribution patterns of the eggs is required to devise an egg production method for the saury.

Lo (1985) calculated the time series of egg production at fertilization of the northern anchovy in 1951–82. Year-to-year difference in the egg production was more than 1,000-fold, which is much larger than the difference in saury larval production at hatching in our study, about 33-fold. She also calculated mean yolk-sac larval abundance for the years that showed a difference of more than 1,000-fold. Annual fluctuation of reproductive level in the saury seemed to be smaller than the northern anchovy. This might be related to the differences in spawning ecology of these two species. The saury is reported to be a multiple spawner that spawns in 2 mo intervals in the spawning season (Hatanaka 1955) with a batch fecundity of 500–3,000 egg/female (Hatanaka 1953). The spawning frequency is 3–5 times/yr and the annual fecundity is estimated to be 1,500–15,000. In contrast, time between spawning incidence of the northern anchovy off southern California is 6–8 days and the batch fecundity is 389 eggs/g of ovary free female body weight (Hunter and Goldberg 1980). The saury is less fecund than the northern anchovy and seems to be less variable in its annual fecundity owing to a long maturation period of ovarian eggs. Small year-to-year differences in the reproductive level in the saury might be the result of less variable spawning effort.

The correlation of the larval production at hatching and the daily IMR in the individual years may indicate that the mortality of young saury is density dependent. Watanabe (1987) showed an inverse correlation between the egg abundance and the overall survival rate of larval and juvenile Japanese sardine up to 1 yr old. He further examined correlations between the egg abundance and the biomass of larvae of the 40 mm size class, and between the biomasses of the 40 mm size class and of the 1 yr recruit size class. He found that egg abundance and survival rate up to 40 mm size class are inversely correlated, whereas the biomass of the 40 mm and 1 yr size class are positively correlated. His conclusion was that the mortality rate of larval sardine is density dependent up to 40 mm. Thus, in some pelagic fish, mortality rates of early life stages could be density dependent.

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Bluefin Tuna, *Thunnus thynnus*, Larvae in the Gulf Stream off the Southeastern United States: Satellite and Shipboard Observations of Their Environment

Michael F. McGowan and William J. Richards

ABSTRACT: The primary spawning area of the western Atlantic stock of bluefin tuna is presumed to be in the Gulf of Mexico. However, bluefin tuna larvae were collected in April and May 1985 along the shelf edge from Palm Beach, Florida to Cape Fear, North Carolina and offshore as far as 260 km east of Jacksonville, Florida over the Blake Plateau. Satellite and shipboard sea-temperature data indicate that the larvae over the shelf edge were advected there in meanders of the Gulf Stream. Bluefin larvae previously reported in the Straits of Florida and off Cape Hatteras were also in the Gulf Stream according to retrospective analyses of temperature and salinity data. Based on age-length relationships and current velocity, one small larva was probably spawned north of Miami, Florida while others could have been advected into the Gulf Stream from the eastern Gulf. Spawning by a few unspent migrating adults could also account for some bluefin larvae in this region. The estimated total larvae off the southeastern United States in 1985 could have been produced by 5% of the spawning stock. Bluefin larvae were found within a narrow range of sea surface temperatures and salinities at offshore stations. Preliminary assessment of larval habitat indicates that waters off the southeastern United States are unfavorable for growth and survival of bluefin larvae relative to hypothesized larval retention areas in the Gulf of Mexico.

The western Atlantic stock of bluefin tuna, *Thunnus thynnus*, spawns from about mid-April to mid-June in the Gulf of Mexico, based on seasonal and areal distribution of their larvae (Richards 1976, 1977). Bluefin tuna larvae have also been collected in the Straits of Florida north of Cuba and east of Miami (Richards and Potthoff 1980; Brothers et al. 1983) and off Cape Hatteras, NC (Berrien et al. 1978).

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Surveys of the Gulf of Mexico for bluefin tuna larvae are made annually during the spawning season to estimate the total abundance of larvae and to calculate a fishery-independent index of adult spawning stock size (Richards et al. 1981; McGowan and Richards 1986). This index of stock size is used to calibrate virtual population analysis (VPA) of the western Atlantic bluefin tuna population to enhance management of the stock (Anonymous 1986). Fishery catch statistics and the index of abundance of larvae show that the bluefin tuna population size is smaller than it was previously, and is below optimum levels (Brown and Parrack 1985; McGowan and Richards 1986). To redress this problem, directed fishing on bluefin in the Gulf of Mexico and in other spawning areas, has been prohibited since 1982 (Anonymous 1987).

Finding bluefin larvae outside the primary spawning areas raises a potential problem because if significant spawning of the remaining stock occurs outside the Gulf of Mexico, then the ichthyoplankton survey in the gulf may not give a reliable index of the stock, and prohibition of fishing in the gulf may not have the desired effect on stock recovery. In 1985 bluefin larvae were widely distributed off the southeastern U.S. coast. The hypothesis that they were spawned in this area needed evaluation.

In this paper we quantitatively describe the occurrence of bluefin tuna larvae in 1985 near Miami and Cape Hatteras, where they have been reported before, and also their occurrence over the Blake Plateau north of the Bahamas Islands, where they have not been reported previously. We use satellite observations of the position of the Gulf Stream and shipboard hydrographic measurements to describe the habitat where bluefin tuna larvae were collected. We review previous evidence for bluefin tuna spawning in this area to determine if these larvae were in similar, oceanographically defined habitat, and summarize this evidence to assess the waters of the southeastern U.S. coast and the Blake

Plateau as a spawning area for bluefin tuna. We propose a hypothesis, based on existing data, that bluefin tuna are dependent on a dynamic larval retention area associated with the Loop Current in the eastern Gulf of Mexico.

The total number of specimens of bluefin tuna larvae on which this paper is based is small. Therefore, we present our conclusions as hypotheses that are consistent with our data from independent sources and with all other data known to us. Arguments supporting our hypotheses and their limitations will be elaborated in the discussion.

Our investigations were initiated by the observation of bluefin tuna larvae outside the normal spawning area and then proceeded by a series of questions, critical examination of available information, and conclusions and hypotheses for further investigation. The bluefin tuna larvae off the southeastern U.S. in 1985 could have been spawned locally or transported in currents. Were they in water masses characteristic of the Gulf Stream? If they were in the Gulf Stream, then were they young enough to have been spawned locally or were they transported from upstream? Other researchers had reported incidental catches of bluefin tuna larvae in some of the same areas. Were these larvae likely to have been spawned locally? Wherever they were spawned, could they survive where they were collected? What were the general temperature-salinity conditions where bluefin tuna larvae were found off the southeastern U.S.? Are these conditions similar to those which bluefin tuna larvae experience in the Gulf of Mexico? What else is known about the oceanography of this region which is relevant to survival of fish larvae? Given our conclusions from these data and our knowledge of the life history of the bluefin tuna, what insights can be drawn from the occurrence of larvae outside the presumed spawning area and what hypotheses need to be tested by additional work?

METHODS

Ichthyoplankton were collected on cruise 152 of the RV *Oregon II* in April and May 1985. Double oblique tows to 200 m or to near the bottom in shallow water were made with 0.6 m diameter bongo nets having 0.333 mm mesh size. Bluefin tuna larvae were identified and measured by W. J. Richards. Salinity and temperature data collected by CTD, XBT, or bottle cast at each station were extracted from computer data files of the National Marine Fisheries Service, Mississippi Laboratory, Pascagoula. Satellite data for April and May 1985 were obtained from NOAA Miami SFSS Gulf Stream Position Flow Chart #2450 for the days during the cruise. Historical observations of bluefin tuna larvae and coincident temperature and salinity near Cape Hatteras were obtained from Berrien et al. (1978) and Clark et al. (1969). Previous observations of bluefin tuna larvae outside the Gulf of Mexico were reviewed for other evidence of spawning in the Straits of Florida or elsewhere (Richards 1976; Brothers et al. 1983).

Statistical estimates of standardized abundance of larvae were made using the delta-distribution, an efficient estimation technique when zero counts are observed (Pennington 1983). This is the same method routinely used to construct the fishery-independent index of the abundance of Gulf of Mexico spawners. Because of logistical and statistical sampling problems, the estimates of abundance are best regarded as indices calculated in a consistent way and valid for comparative purposes. Unless there is spatial periodicity or patchiness at the same scale as our sampling grid, the systematic survey does provide, however, an accurate estimate of mean abundance and its variance (Poole 1974; Ripley 1981). The details of the method are provided in McGowan and Richards (1986). The estimate assumed that fecundity, sex ratio, spawning season, and length-weight-age ratios were the same off the southeastern U.S. as in the Gulf of Mexico (Baglin 1982). This assumption was supported by the similarity of length-frequency distributions of incidental catches of adults in the two areas during May 1985. Because our assumptions are important to subsequent arguments, the evidence substantiating our reasoning is given in detail below.

Approximately 90% of incidentally caught adult bluefin tuna in the gulf and off the southeastern U.S. during May 1985 were large, spawning-sized fish >190 cm (data provided by S. Turner, National Marine Fisheries Service, Miami Laboratory). There was no statistical difference in proportion of adult spawners between the two areas (Chi-Square = 0.0176; $P = 0.89$; McGowan and Richards 1987). Thus the available catch data were consistent with our assumption that the fish in both areas were similar in terms of size-related reproductive capacity. This was the primary justification for using reproductive parameters of Gulf of Mexico tuna for calcu-

lations of potential stock size of spawners off the southeastern U.S.

Additional data indicate that there is only one spawning stock in the northwestern Atlantic. Bluefin tuna are known to occur in different places at different times of the year, depending on size and age (Rivas 1978; Mather 1980). The large adults are expected to be migrating through the Straits of Florida during late April and May after spawning in the Gulf of Mexico. A few migrating, ripe females and recently spent males were caught in May near Bimini in the Bahamas (Rivas 1954). Bluefin tuna are capable of swimming from the Bahamas to Norway at sustained speeds as fast as 122 miles per day (Brunenmeister 1980), so adult fish could easily traverse the area from Miami to Cape Hatteras, or be widely distributed over the Blake Plateau, a few days after leaving the Gulf of Mexico. They could migrate back and forth between the two areas during the 60 d spawning season, although there is no evidence for this. Because there is no evidence for two separate groups of spawning fish, the parsimonious assumption is that there is only one. Therefore we assumed that fish in both areas had the same reproductive parameters previously estimated (Baglin 1982; McGowan and Richards 1986).

The estimated age-at-length of bluefin tuna larvae was based on previous analysis of daily increments in otoliths of larval bluefin collected from the Gulf Stream near Miami (Brothers et al. 1983). We calculated a linear regression to predict age from length using the mean estimates of age at length presented in Brothers et al. (1983). The equation is

$$\text{Age (days)} = 3.67 \times \text{standard length (mm)} - 8.04.$$

This equation was based on limited ranges of age and length, so we used it heuristically as the best available. It may be revised after further study extends the age and length data, but the revisions will most likely be at the older-longer end of the relationship, not at the younger-shorter end most relevant to our conclusions in this paper. There is a range of age at length which could affect interpretations of time spent drifting by the larvae but our use of the mean results in conservative interpretations of the data in most instances.

In this paper we refer to the current from the Dry Tortugas to Cape Hatteras as the Gulf Stream (Iselin 1936; Stommel 1965). We refer to the continental shelf area between Palm Beach, FL and Cape Hatteras, NC as either the region off the southeastern United States, or the South Atlantic Bight.

Stations occupied during RV *Oregon II* cruise 152 were numbered 42XXX, where XXX is a sequential station number. For brevity we refer to stations in this paper by their unique 3 digit number, the XXX part.

RESULTS

Catch and Abundance of Larvae

Larval bluefin tuna were collected at 10 of 147 stations during cruise 152 (Fig. 1). Three larvae were collected at one station, two at two stations, and one each at the other positive stations for a total catch of 14 larvae (Table 1). To put this small catch in perspective, in 1984 and 1986 the average catch in the Gulf of Mexico was less than 24 total larvae at 10 positive stations (McGowan and Richards 1987). Thus the 14 caught in 1985 could have been over 50% of the expected catch for the Gulf of Mexico in 1985. The larvae ranged in length from 3.0 to 6.2 mm corresponding in age from 3 to 14.7 days postfertilization. The estimated mean abundance of bluefin tuna larvae from stations at or outside the 183 m isobath was 0.383 ± 0.114 (SE) under 10 m^2 of sea surface (approximately ⅓ the density of bluefin larvae in the Gulf of Mexico). The corresponding area surveyed was 2.02×10^{11} m^2 producing a total estimated 7.74×10^9 larvae in the survey area. These larvae could have been produced by 3,730 adult fish weighing a total of 903 t. This is equivalent to about 5% of the 1985 estimate of Gulf of Mexico spawning stock calculated from the larval index (McGowan and Richards 1987). The coefficient of variation of the estimate of abundance of these larvae was 30%, which is in the range of coefficients of variation for the Gulf of Mexico for the past 10 years, 21–49% (McGowan and Richards 1987).

Distribution of Bluefin Tuna Larvae and Coincident Water Masses

There were three groups of stations where bluefin tuna larvae were present: 1) three stations at the shelf break east of Florida, 2) two stations near the shelf break off North Carolina, and 3) the positive stations over the Blake Plateau. The stations in the first group (634, 636, and 647) were near the 183 m isobath. Two inde-

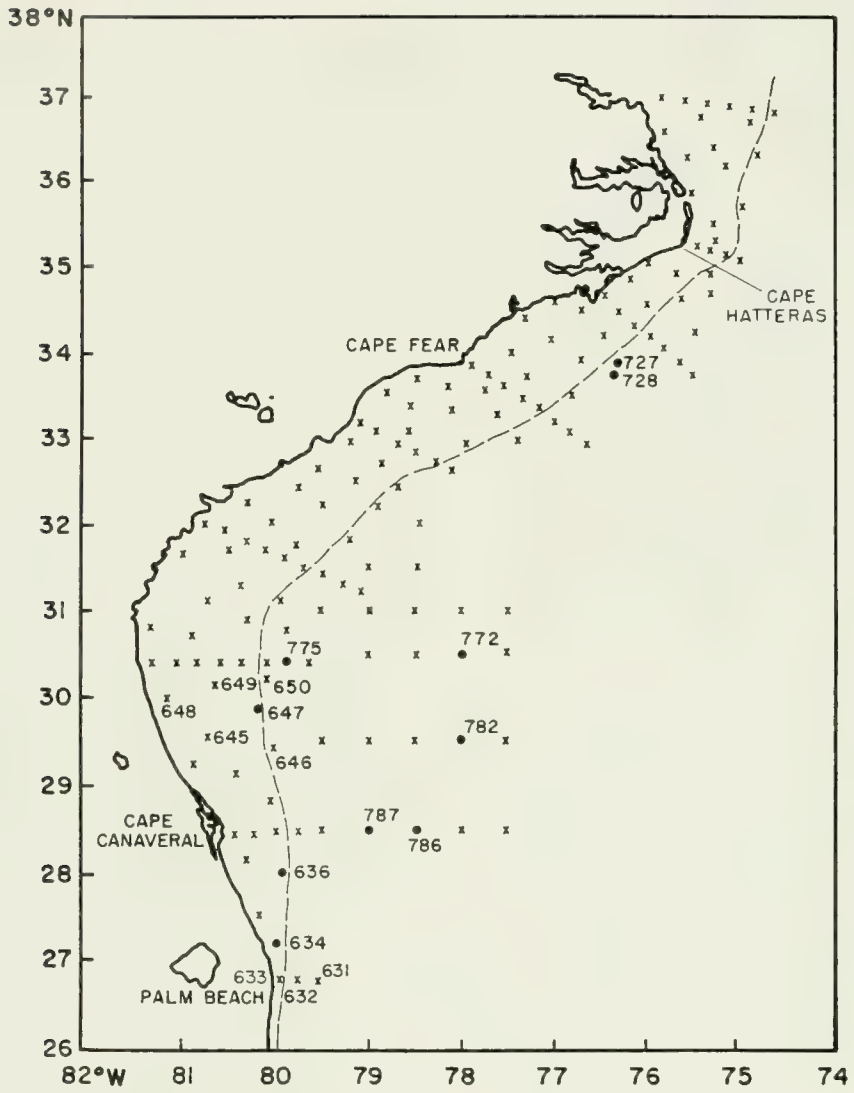

FIGURE 1.—Study area with ichthyoplankton and hydrographic stations plotted, and selected stations numbered. Stations where bluefin tuna larvae were present are indicated by a heavy dot. The dashed line shows the position of the 183 m isobath.

pendent sets of data, temperature-depth profiles, and remote sensing images of surface temperature, show that the water at these stations when bluefin tuna larvae were caught was the shoreward edge of the Gulf Stream. Temperature profiles of stations 631, 632, and 633 (Fig. 2) show cold water is closer to the surface at the inshore station (633) than at the offshore stations (631, 632). This is typical at the cold edge of the Gulf Stream near the shelf break (e.g., Atkinson 1985). Station 634, where bluefin tuna larvae were present, is a little inshore and north of station 633. Its vertical temperature profile shows warm Gulf Stream water at the surface and the cold water of the edge of the stream closer to the surface than at station 633. Station 636, where bluefin tuna larvae were present also, has a similar temperature profile. The upper mixed layer at stations 634 and 636 is approximately 30 m deep like that at station 633, not 60–80 m deep as at station 631 which was farther offshore. These temperature profiles are typical of the edge of the Gulf Stream at this latitude (Atkinson et al. 1987).

The third positive station in this group of stations at the shelf edge is station 647. No observations of temperature with depth were obtained at this station but measurements at adjacent

TABLE 1.—Stations where bluefin larvae were present on *Oregon II* Cruise 152, April and May 1985.

Station	Date	Time	Latitude	Longitude	Depth (m)	Catch	Length (mm)
42634	4/27	1035	27°10.5′	79°51.1′	70	1	4.0
42636	4/27	1732	27°58.2′	79°59.6′	122	3	5.6
							6.1
							6.2
42647	4/29	524	29°51.9′	80°12.3′	210	1	3.8
42727	5/14	1043	33°51.0′	76°17.0′	366	1	5.8
42728	5/14	1445	33°44.0′	76°19.0′	561	1	3.0
42772	5/21	2200	30°30.0′	78°0.0′	842	2	3.0
							4.2
42775	5/22	900	30°24.0′	79°39.0′	732	1	5.7
42782	5/23	1515	29°30.0′	78°0.0′	843	1	4.0
42786	5/24	1100	28°30.0′	78°30.0′	950	1	4.5
42787	5/24	1314	28°30.0′	79°0.0′	846	2	3.7
							4.9

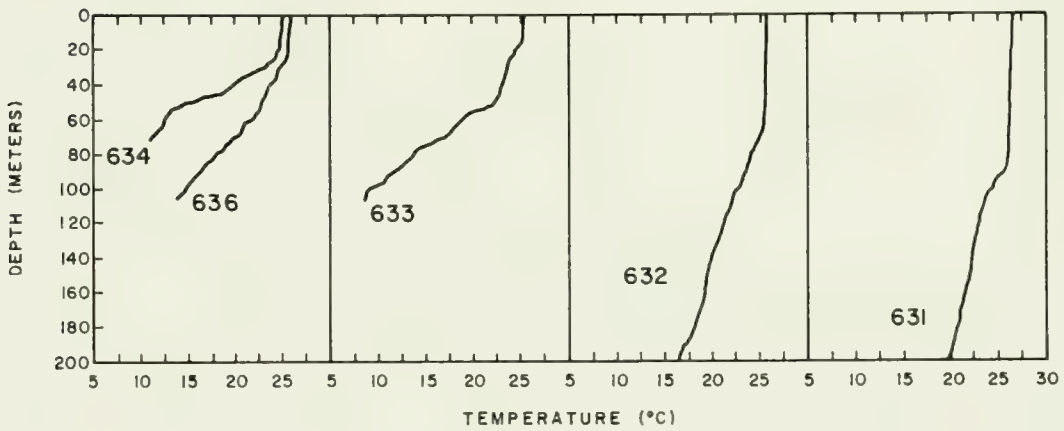

FIGURE 2.—Temperature-depth profiles of selected stations in the southern part of the study area. Stations 631, 632, and 633 are along an east to west transect at the edge of the shelf (see Figure 1). The edge of the Gulf Stream is indicated by colder water near the surface inshore at station 633. Bluefin larvae were collected at stations 634 and 636 where the profile is similar to that at 633.

stations are useful as proxies. Station 646, which was south and a little offshore from 647, shows a vertical temperature profile (Fig. 3) typical of the Gulf Stream, similar to that at 631 (Fig. 2). Station 650, at a similar isobath and distance from the shore, also shows a temperature profile similar to 631 and 632. Therefore station 647 would reasonably be expected to be more similar to 646 and 650 than stations 648, 645, and 649, which are farther inshore. These temperature profiles indicate that Gulf Stream water was present at stations 634, 636, and 647 when bluefin tuna larvae were collected there.

This conclusion is supported further by charts of satellite data showing the position of the edge of the Gulf Stream. The edge of the stream was just offshore of the 183 m isobath on 26 April, the day before the bluefin tuna larvae were collected at stations 634 and 636 (Fig. 4). The edge was inside the 183 m isobath and inshore of the three stations three days later on 29 April, when bluefin tuna larvae were collected at station 647 (Fig. 5). The satellite-detected temperature front associated with the inshore edge of the Gulf Stream is known to be in accord with the classical definition of the stream path (Olson et al.

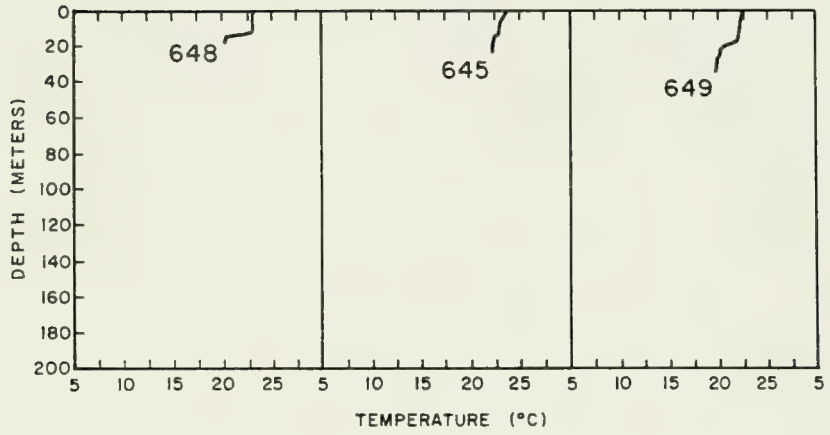

FIGURE 3.—Temperature-depth profiles of stations 646 and 650, which are presumed to represent the profile at station 647. Bluefin larvae were collected at 647 but no hydrographic data were collected there. Profiles for

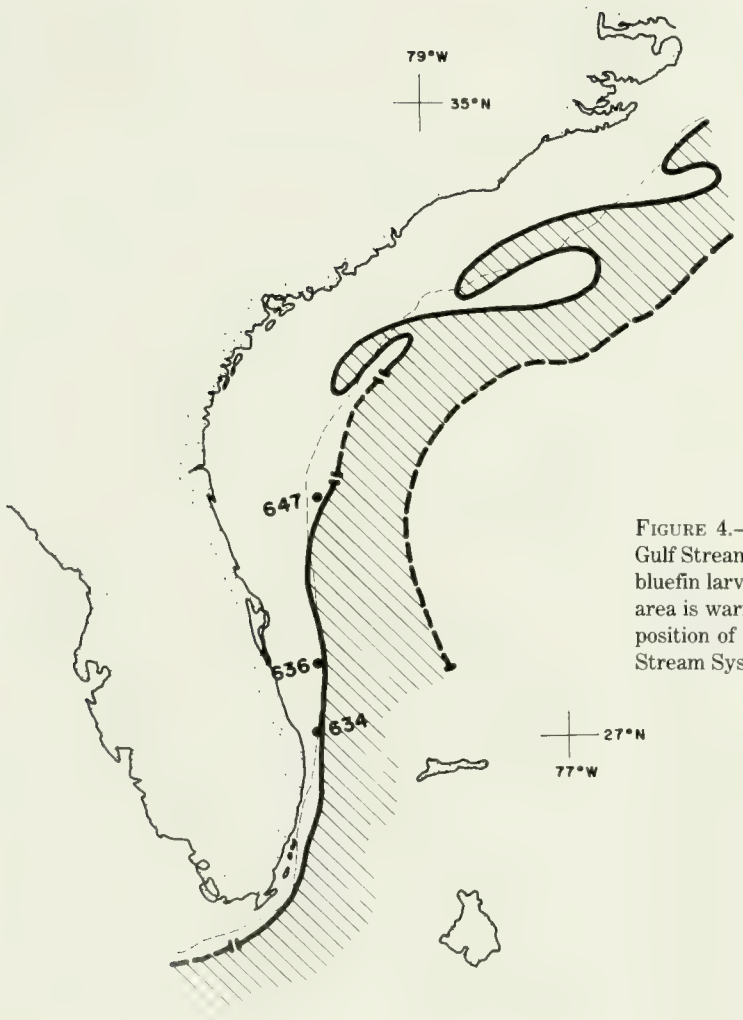

FIGURE 4.—Chart showing the position of the edge of the Gulf Stream on 26 April 1985 relative to three stations where bluefin larvae were collected 27–29 April. The cross-hatched area is warm Gulf Stream water. The dashed line shows the position of the 183 m isobath. (Redrawn from NOAA Gulf Stream System Flow Chart #2450, 26 April 1985.)

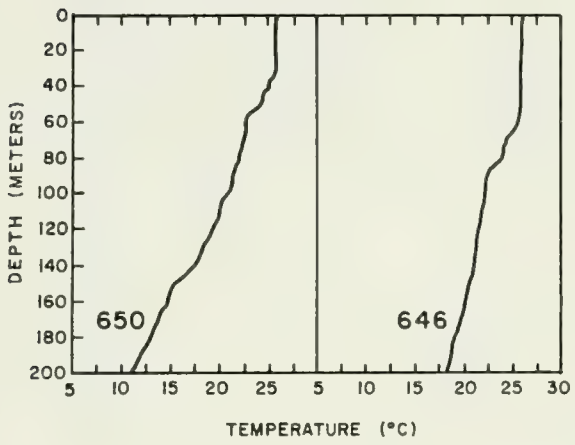

FIGURE 3.—*Continued*—stations 645, 648, and 649, are presumed not to represent conditions at 647 because they are farther inshore.

1983). The inference to be drawn from this remote sensing data is that during 27–29 April the Gulf Stream meandered inshore of the 183 m isobath in this region carrying bluefin tuna larvae over the shelf edge. This is worth noting with regard to the larval habitat of the bluefin tuna because the larvae are rarely taken in water <200 m deep. For example, in the Gulf of Mexico during 1977–81 only 5 of 81 stations that had bluefin tuna larvae were in water <200 m deep and none was in water <110 m deep. (Southeast Fisheries Center, National Marine Fisheries Service, unpubl. data.)

The second group of stations where bluefin tuna larvae were caught is the pair of stations east of Cape Fear, NC where the water depth was 360–560 m (stations 727 and 728). Water temperatures at the surface, at 100 m, and at 200 m were similar to temperatures at the same depths for other Gulf Stream stations such as

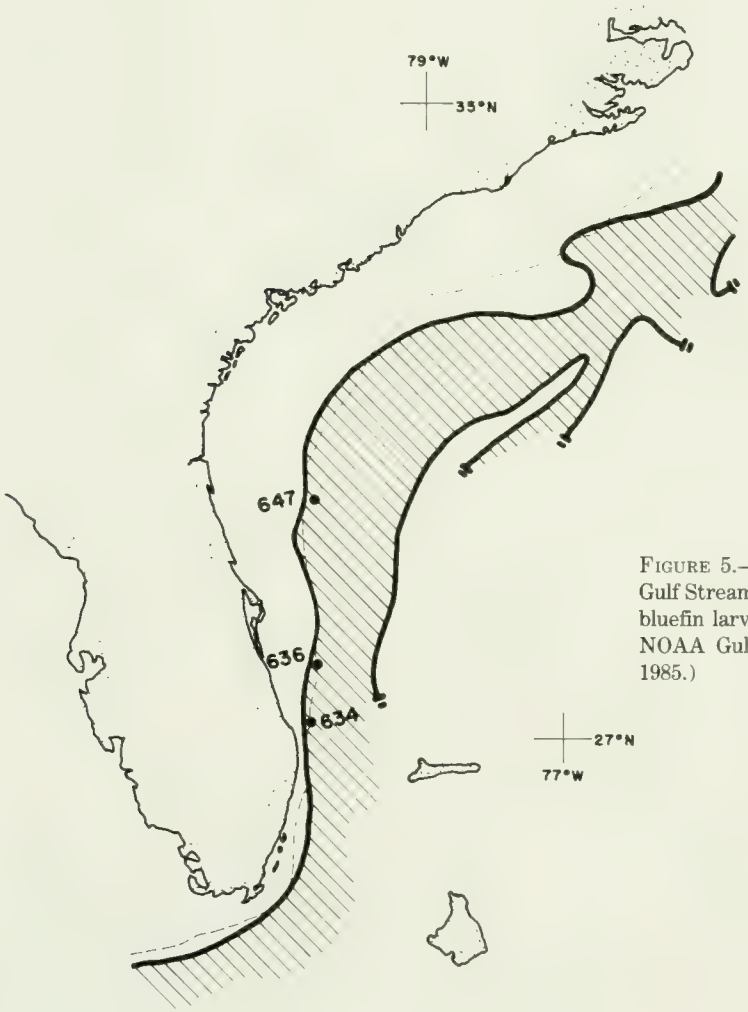

FIGURE 5.—Chart showing the position of the edge of the Gulf Stream on 29 April 1985 relative to three stations where bluefin larvae were collected 27–29 April. (Redrawn from NOAA Gulf Stream System Flow Chart #2450, 29 April 1985.)

station 631 and 632 (Table 2). Station 727 was located at a shallower isobath than station 728 and the temperature at depth readings were similar to those 800 km south, at stations 632 and 631, where the water depth was similar. At both pairs of stations cold water is nearer the surface of the inshore station. The sloping isotherms and the temperatures at depth are characteristic of the edge of the Gulf Stream. Gulf Stream water is expected here in spring and summer (Pietrafesa et al. 1985).

Remote sensing observations (Figs. 6, 7) show that remnants of a filament of warm water resulting from an earlier onshore meander were still present when these larvae were collected. Upwelling is associated with onshore meanders of the Gulf Stream and cyclonic eddies are formed between the warm filament and the Gulf Stream. The bluefin tuna larvae at stations 727 and 728 were not over the shelf in a patch of productive water caused by the onshore meander, but they were in an area which could have been fertilized by such a patch which subse-

TABLE 2.—Temperature with depth comparison of northern stations where bluefin larvae were present and southern stations which were at the same isobath and in Gulf Stream water. Bluefin were collected at stations 727 and 728. Stations 728 and 631 were offshore (Fig. 1.). Note that 22° at 100 m is a good indicator of the Loop Current (Liepper 1970) which flows from the Gulf of Mexico to join the Gulf Stream.

	Temperature (°C)			
	Northern stations		Southern stations	
Depth (m)	727	728	632	631
0	25.8	26.2	26.1	26.8
100	21.8	22.5	21.6	23.6
200	16.7	19.2	16.7	19.5

FIGURE 6.—Chart showing the position of the edge of the Gulf Stream on 13 May 1985 relative to two stations (727 and 728) where bluefin larvae were collected 14 May. Note the three filaments left by meanders of the Stream. These can enclose cold cyclonic eddies. (Redrawn from NOAA Gulf Stream System Flow Chart #2450, 13 May 1985.)

quently moved offshore. A 3.0 mm bluefin larva estimated to be only three days old was collected here at station 728.

The third group of stations with bluefin tuna larvae were all farther offshore in water more than 700 m deep. The surface water here had a narrow range of salinities from about 36.0 to 36.5 ppt. Temperature at the surface in this region ranged from approximately 24.5° to 27.5°C. Bluefin tuna larvae were found where the surface water was in the center of this temperature range: from 25.5° to 26.5°C. Bluefin tuna larvae from the northern positive stations and the southern shelf edge stations were also found at the same surface salinities and temperature, except for station 634 where the temperature was 24.8°C (Fig. 8).

Previous Captures of Bluefin Tuna Larvae off Cape Hatteras

In 1966 three bluefin tuna larvae were collected off Cape Hatteras (Berrien et al. 1978). One larva 7.7 mm long was collected 20 April in 235 m water depth. Two larvae, 5.4 mm and 9.3 mm SL, were collected 23 June over 269 m and 68 m, respectively. The stations where these larvae were collected are at the shelf edge or just inshore of it. Contour plots of surface temperature (Fig. 9) and salinity (in Berrien et al. 1978) show that the Gulf Stream front was inshore of the stations where bluefin larvae were caught. Temperature cross-sections show clearly that the stations where bluefin tuna larvae were collected were in Gulf Stream water (Fig. 9). The larva caught in April was in water with lower surface temperature and lower surface salinity than typical (Fig. 8) for the stations where bluefin tuna larvae were present in 1985. The two larvae caught in June were in water more typical for bluefin tuna larvae but near the highest salinities and temperatures (Fig. 8).

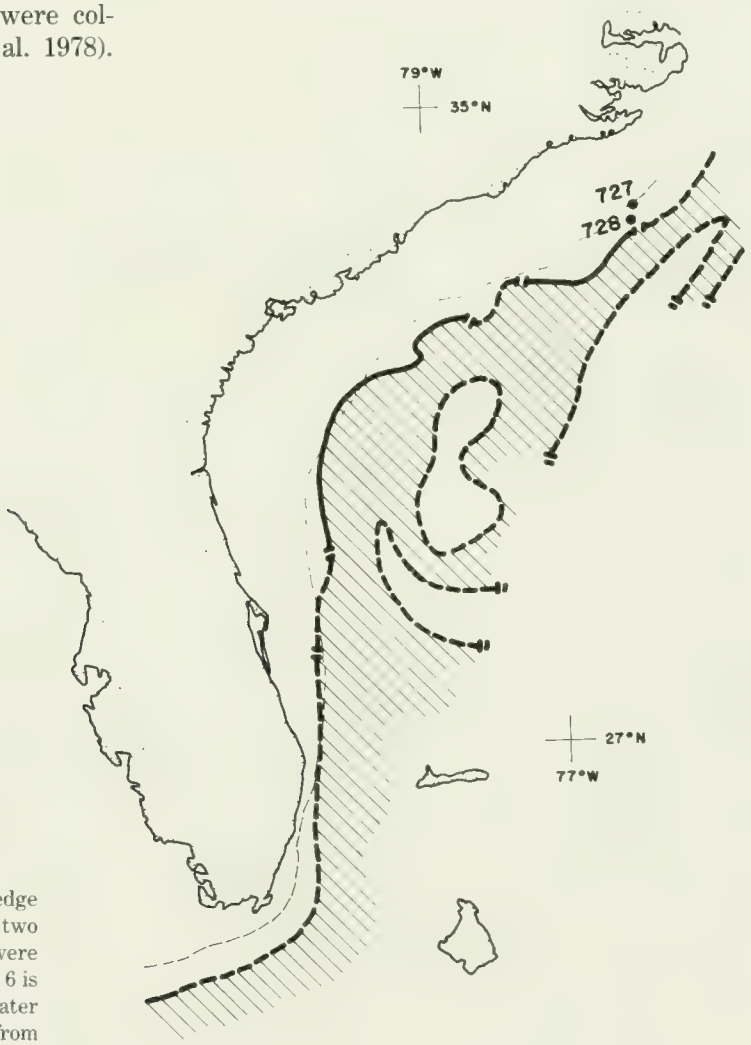

FIGURE 7.—Chart showing the position of the edge of the Gulf Stream on 15 May 1985 relative to two stations (727 and 728) where bluefin larvae were collected 14 May. The filament shown in Figure 6 is not visible and the stations are now in colder water inshore of the edge of the Stream. (Redrawn from NOAA Gulf Stream System Flow Chart #2450, 15 May 1985.)

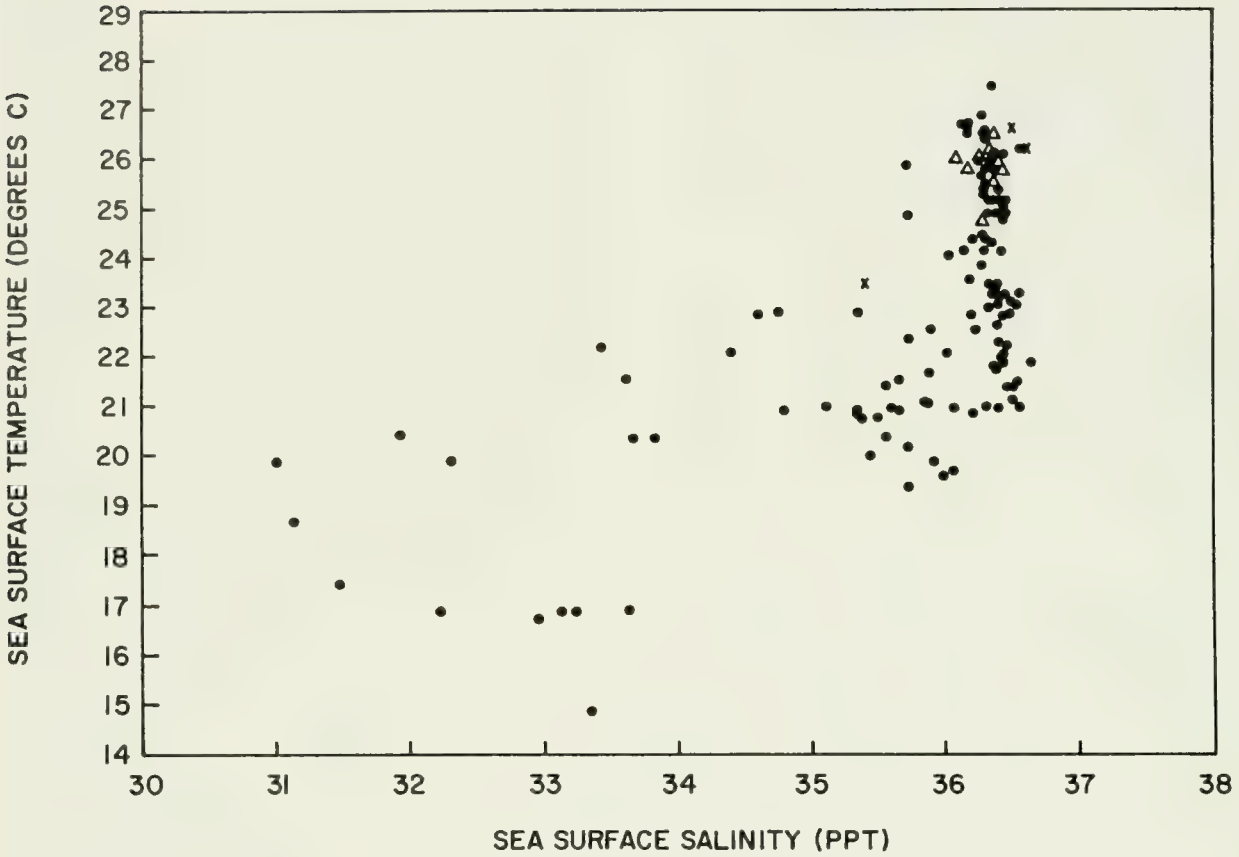

FIGURE 8.—Plot of sea surface temperature vs. sea surface salinity for stations on the cruise which had observations of both. Stations with bluefin larvae are plotted as open triangles. The three x's show the surface temperature and salinity of the stations near Cape Hatteras where bluefin larvae were collected by Berrien et al. (1978).

Previous Captures of Bluefin Tuna Larvae off Miami

Bluefin tuna larvae were collected in 1969–71 and in 1975 between Miami and the Bahamas by Richards (1976). On a five-station transect between Miami and Bimini Bahamas (Richards 1976, table 2), 82% (32/39) of bluefin tuna larvae taken in neuston tows were taken at two stations. These two stations were located on the Miami side of the center of the Florida Straits where the high velocity core of the current is located on average (e.g., Stommel 1965:139). All of the bluefin tuna larvae taken in bongo tows along the transect were taken at the same two stations where most of the neustonic specimens were collected. All of these larvae were longer than 3.0 mm, older than 3 days, so that, if they were advected at the mean current velocity in this location, 100 km d^{-1} (Fuglister 1951), they would have been spawned west of Key West, FL (long. 82°W).

In 1981, 369 bluefin tuna larvae were collected off Fowey Light, south of Miami, at approximately lat. 25.6°N (Brothers et al. 1983). The collections were made on four days, 19–21 May and 2 June, using 1 m diameter or 1 × 2 m neuston nets which were towed many times each day. No oceanographic data were collected because the purpose of the sampling was to capture specimens for otolith ageing, but the collections were made "5–10 miles offshore in blue water at the edge of the Stream" according to E. D. Prince.[1] Based on satellite observations during this period (NOAA Gulf Stream System Flow Chart #2450), the edge of the Gulf Stream was offshore of the 183 m isobath (which is 5–10 miles offshore near Fowey Light) on 18 May, was at the 183 m isobath 20 May, and was offshore again 22 May. Nearly half of the total catch (176/369) of bluefin tuna larvae during four days of sampling took place on 20 May (Brothers et al.

[1]E. D. Prince, Southeast Fisheries Center Miami Laboratory, National Marine Fisheries Service, NOAA, 75 Virginia Beach Drive, Miami, FL 33149, pers. commun. 1988.

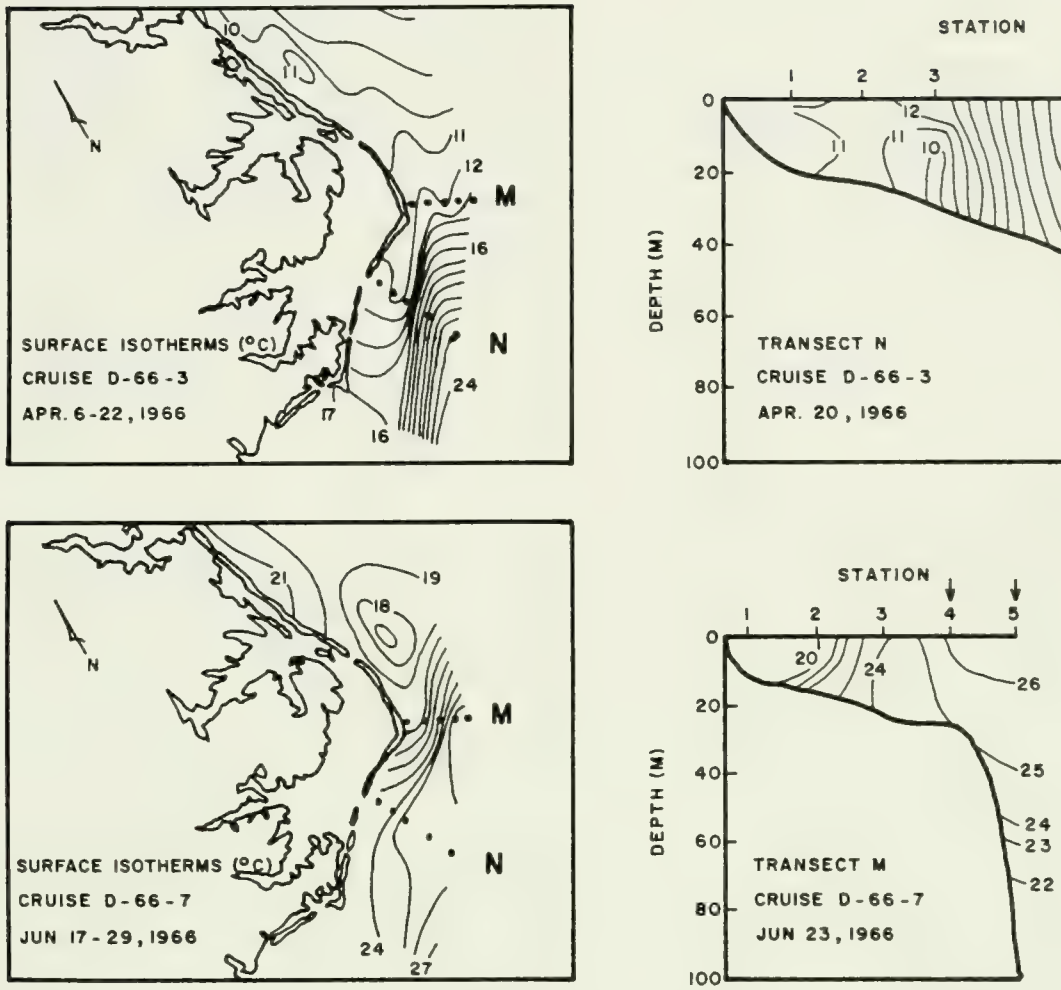

FIGURE 9.—Plots of surface isotherms and temperature sections of the stations where bluefin larvae were collected near Cape Hatteras by Berrien et al. (1978). The plot at upper left shows the position of the temperature front at the sea surface between stations 3 and 4 on transect N. The section at upper right shows that the front extends to the bottom; station 5, where a bluefin larva was collected, is indicated by an arrow. Plot at lower left shows the surface front inshore of station 4 on transect M. Section at lower right shows temperatures; the two stations where bluefin larvae were caught are indicated by arrows. (Figures redrawn from Berrien et al. 1978.)

1983:50), the day when the Gulf Stream was at its closest inshore position during the sampling days. Thus nearshore catches were highest when the rapidly flowing core of the Gulf Stream meandered toward shore, carrying bluefin tuna larvae with it.

DISCUSSION

Limitations of the Data

Bluefin tuna larvae are rare on the average in their oceanic habitat. Standard ichthyoplankton tows, which are made to 200 m in order to quantitatively sample all species, undersample the surface layers where tuna larvae are more abundant. In addition, we have evidence, to be published elsewhere, that bluefin tuna larvae are most abundant near specific oceanographic features; so they may be undersampled by nonstratified survey designs such as the uniform grid often used for logistical reasons. The estimates of abundance will be valid but may have wider confidence intervals than estimates made with a more efficient stratified design. Furthermore, bluefin tuna larvae grow and swim rapidly, so they avoid plankton nets better than larvae of most other species, again contributing to low absolute catches. We acknowledge that low catches limit the precision of results; therefore, we tried to rein in unwarranted speculation. The calculations of adult biomass from larval abun-

dance are made only for comparative purposes. A recent independent review of our techniques concluded that the index of larval abundance probably reflects trends in abundance of adults accurately but that our ad hoc estimate of adults from the larvae resembles VPA estimates coincidentally because of our choice of a larval mortality rate. Our ongoing research is aimed at improving the precision and accuracy of estimates of abundance of bluefin tuna larvae by combining our increasing knowledge of their biology with improved sampling gear and methods.

Nevertheless, we are confident that our interpretation of the preceding data is justified and reasonable because of decades of accumulated experience with this species, because of the variety of independent sources of data which are consistent with our interpretations, and principally because the most important conclusions and hypotheses presented here are not dependent upon quantitative estimates of abundance, but upon the relationship between presence and absence of bluefin tuna larvae with specific oceanographic variables. Despite our confidence in our presentation of the results we readily admit that additional data could falsify our conclusions.

Assessment of Spawning off the Southeastern United States

Assuming that all the larvae caught near the shelf and over the Blake Plateau were spawned near where they were collected, spawning in the area was only a small fraction (5%) of estimated total spawning by the western Atlantic stock (McGowan and Richards 1987). This is similar to a previous estimate (6%) of the number of ripe females passing the Bahamas during May (Rivas 1954:310). However, because of the currents in this region, it is not certain that the larvae were spawned near the area where they were collected.

Currents along the outer shelf off the southeastern U.S. average 0.5–1.0 m s^{-1} during the summer (Atkinson and Menzel 1985). Gulf Stream surface currents off Florida based on ship drift observations during April–June average 1.5 m s^{-1} or less (Fuglister 1951). During April–June 1985 the mean northward current, measured at 29°N and at 30 m depth over the 75 m isobath, was 0.53 m s^{-1} and the maximum current was 1.55 m s^{-1}, approximately 3 kn (Lee et al. 1986). Current velocity at the wind-affected surface and farther offshore in the fastest moving region of the Gulf stream would be higher.

If we use the long-term average of 1.5 m s^{-1} as the mean northward speed of the surface current, then a planktonic fish larva would travel 116 km in one day. The mean distance travelled in 7 days would equal 812 km which is less than the straight-line distance from Cape Hatteras, NC (35°N, 76°W) to Palm Beach, FL (27°N, 80°W), approximately 970 km. These calculations suggest that larvae <7 days after fertilization, which were found as far north as Cape Hatteras, could have been spawned north of the Straits of Florida. Those more than 7 days old, or larger than about 4 mm (minimum size at this age, not mean; see Brothers et al. 1983), could have been spawned in the Straits of Florida or the southeastern Gulf of Mexico. Ten of the 14 larvae collected in 1985 were 4.0 mm or longer, and most of the larvae were caught far south of Cape Hatteras. Therefore, based on current velocity and estimated ages, most of the bluefin tuna larvae were probably not spawned off the southeastern U.S. near the area where they were collected.

The 3 d old (3.0 mm) bluefin tuna larva collected near lat. 34°N could not have been spawned in the Gulf of Mexico because, even at 2.5 m s^{-1}, it would have travelled only 667 km in three days. A 667 km straight line from where the larva was caught would end at about 28°N, which is north of Palm Beach. However, the interpretation must be different for the larger, older larvae. Except for the single 3 mm larva, those in the high velocity core of the Gulf Stream (at the shelf edge) could have been advected from a distance to the south in only a few days. At only 1.0 m 5^{-1} (a little faster than 2 kn) larvae 4–5 mm long, corresponding to approximately 8 days old, could have been advected from off Miami to about 31°N in 5 days. The larvae collected along the shelf edge and over the Blake Blateau in 1985 were in this size range or a little longer. Therefore all but the 3 mm larva could have been spawned in the southeastern Gulf of Mexico or between the Florida Keys and Cuba. Slow growth due to cold-water temperature could explain small larvae far from their spawning area, but in this case the Gulf Stream water was warmer than the water where bluefin tuna larvae were found in the Gulf of Mexico.

It should be noted that the current circulation east and north of the Bahamas is complicated

(Olson et al. 1984). Gyres and slow recirculation in this area could retain fish larvae for several days. This means that the evidence presented here does not eliminate the possibility that bluefin tuna spawn off the southeastern U.S. However, because larvae collected in rapidly moving water were probably transported in that water, we argue that the data support the contention that the primary spawning area is farther upstream with perhaps some late spawning by a few individuals in the Straits of Florida as suggested by Rivas (1954).

Oceanic Habitat of Bluefin Tuna Larvae

Four aspects of larval fish habitat are important to the survival of individuals and recruitment to the adult stock: thermal and salinity conditions, prey, predators, and patterns of ocean circulation that can retain the larvae in favorable areas. Our data do not permit discussing the predators coincident with the bluefin tuna larvae found off the southeastern U.S., but we can discuss the salinity and temperatures, the food potentially available, and the likelihood of retention in a favorable area.

Surface salinity over the shelf of the southeastern U.S. is generally 35 ppt or less, with peak river runoff in spring affecting the central and inner shelf (Atkinson and Menzel 1985). Salinities over the outer shelf are similar to those in the Gulf Stream (35.0–36.5 ppt; Stommel 1965). Salinity lower than full-strength seawater could be potentially detrimental to larval bluefin tuna although the adults tolerate reduced salinities (Topp and Hoff 1971). All the larvae collected in this study were found within a narrow range of salinity near 36 ppt (Fig. 8). The larvae were also found in a fairly narrow range of temperatures near 26°C (Fig. 8). In the Gulf of Mexico in 1984 and 1986, bluefin tuna larvae were found where sea surface temperature (SST) ranged from 22.0° to 28.1°C. More than 87% of the larvae occurred in a narrow range of temperatures between 24.0° and 26.1°C (Southeast Fisheries Center, National Marine Fisheries Service, unpubl. data). This is similar to the temperature range off the southeastern U.S. where bluefin tuna larvae were found at SST's from 24.7° to 26.5°C However, the mean temperature of occurrence of the bluefin tuna larvae was higher here than in the Gulf, 25.72° vs. 24.99°C (t = 2.98; df = 50; $P < 0.005$). At higher temperature metabolic requirements of the larvae would be higher; larvae would require more food for optimal growth and survival, other conditions being equal.

A potential mechanism for producing larval fish food does exist in this region. Onshore meanders of the Gulf Stream along the southeastern U.S. can cause upwelling of nutrient rich water along the shelf edge (Yoder et al. 1981; Yoder 1983). This and the compression of isotherms near the edge of the Gulf Stream might produce a stable stratified region favorable to the growth and to the persistence of patches of larval fish food (Lasker 1981). It is true that intrusions of cold, upwelled water provide pulses of phytoplankton production on the shelf which initiate the formation of patches of zooplankton (Paffenhofer et al. 1987). However, these isolated patches are most often produced in July, when winds as well as currents are favorable for upwelling. Furthermore, the zooplankton in the patches consist primarily of small species of copepod and gelatinous salps and doliolids which are most abundant in cool water near the bottom and in the thermocline. Small copepods are not ideal food for larval bluefin which eat other larval fishes. Larval fishes were not noticeably abundant in the patches; however, the sampling gear used by Paffenhofer et al. (1987) was not optimal to catch fish larvae. The gelatinous zooplankters which can be predators of fish larvae pose a potential hazard to the tuna larvae. Therefore the patches of plankton on the shelf caused by onshore meanders of the Gulf Stream do not appear to be favorable habitat for the feeding or survival of bluefin tuna larvae. These isolated patches on the shelf probably benefit benthic filter-feeders more than larval fishes.

Not all meanders that cause upwelling may result in isolated patches on the shelf. A pulse of upwelled, nutrient rich shelf-break water could move offshore, be entrained in the Gulf Stream, and increase the local productivity of near-surface water, thus enhancing the offshore habitat for larval fishes. Longhurst (1983) suggested that surplus production occurs on continental shelves. Walsh et al. (1987) detected export of phytoplankton from the Mid-Atlantic Bight during a spring plankton bloom. Sherman et al. (1984) found that peak spawning for some species is related to topographic features and circulation, and is synchronized with production of the copepod prey of their larvae. Something about the two stations with bluefin tuna larvae off North Carolina in this study (Figs. 6, 7) may have resembled "good" spawning habitat enough to induce migrating adult bluefin tuna to spawn

nearby. Phytoplankton patches can seed other downstream patches in eddies (Heywood and Priddle 1987). This would be favorable for larval tunas offshore of the Gulf Stream front if these patches produced a food chain containing their prey. Much of the eddy-induced production may be flushed offshore rather than contribute to the shelf food chain (Walsh 1986). However, a pulse of nutrients from shelf-edge upwelling would be diluted rapidly by mixing with the Gulf Stream. We need more quantitative knowledge of the trophic results of these linkages between the shelf break and the Gulf Stream and more information about the food requirements of larval bluefin before the potential benefits of shelf-break upwelling to epipelagic ichthyoplankton can be assessed.

Dynamic Larval Retention Areas

Bluefin tuna larvae have been collected over wide areas of the Gulf of Mexico. They appear to occur primarily where currents or eddies encounter the shelf between the 100 and 1,000 m isobaths (Sherman et al. 1983). They may be most abundant at the cold edge of the Loop Current surface fronts in the eastern Gulf of Mexico (Richards et al. in press). Variability in the Loop Current (Sturges and Evans 1983) will produce variability in the seasonal occurrence and amount of such habitat for the bluefin tuna larvae in the Gulf. The amount of habitat may limit the number of bluefin tuna recruits to the adult stock as has been hypothesized for Atlantic herring stocks (Iles and Sinclair 1982). Because it is outside the rapidly flowing Loop Current which feeds into the Gulf Stream, this habitat may be a larval retention area of bluefin tuna. In the larval retention hypothesis developed for Atlantic herring (Sinclair and Iles 1985), the larvae do not undergo development while drifting passively (e.g., Harden-Jones 1968). Instead, they develop into juveniles within a retention region and then migrate actively to juvenile nursery areas.

Bluefin tuna larvae seem to fit into this life history model. Larvae spawned in the Loop Current can be advected to the Gulf Stream off the southeastern U.S. where habitat is relatively unfavorable. Larvae just outside the Loop Current in the Gulf of Mexico retention areas could develop until they are mature enough to begin their migration to feeding areas along the middle and northern U.S. east coast.

The limited data on distribution of bluefin tuna young of-the-year support this hypothesis. Juvenile bluefin tuna appeared in diets of terns at the Dry Tortugas (24°30′N, 82°50′W) from early June to early July (Potthoff and Richards 1970). These juveniles ranged in length from 25 to 115 mm with all sizes present early in the season but only longer ones present later. No juvenile bluefin tuna were noted in April or May during eight years of observations although juveniles of other species of tuna were being eaten by terns during May. The juvenile bluefin tuna were apparently unavailable within the 24 km feeding range of the terns (Robertson 1964) until they began migrating through the Straits of Florida in June. The timing of the migration suggests that there is a distinct and discrete time for the young-of-the-year juveniles to migrate from their larval retention area to their juvenile habitat. Perhaps the larvae must develop enough to begin schooling just as herring do before they begin their migration. Migration by schools of newly transformed juveniles is consistent with the cohesive migration of other age classes of bluefin tuna (Brunenmeister 1980; Mather 1980). Larvae that were swept out of the Gulf in April and May would not be in synchrony with the migration of their year class in June and July unless they reached suitable retention areas off the southeastern U.S. There is no evidence for such areas. The larval retention areas thus play a dual role for bluefin tuna by supplying habitat for larval development and by affecting the timing of migrations of different life stages of the species. The larval retention areas we propose for bluefin tuna and other oceanic pelagic fishes differ from those of fixed size proposed for herring stocks because they are dynamic, varying in date of occurrence, geographical location, and area. This variability in the quantity of larval habitat is a density-independent environmental factor which may explain a significant amount of variability in recruitment of pelagic fishes. Variations in the quality of larval habitat (coincident prey and predators) would cause density-dependent effects within the constraints of the total larval retention habitat.

A quantitative knowledge of bluefin tuna larval retention areas will have two practical applications. The precision of larval surveys, which are the only current independent estimates of the spawning stock, may be improved by a stratified sampling design once the strata of low and high abundance can be defined. In addition, hypotheses about the importance of appropriate habitat for bluefin tuna and the effects on

recruitment of its temporal and spatial variability can be tested by comparing the fishery independent-variations in habitat with recruitment indices based on the catch statistics of commercial and recreational fisheries.

CONCLUSIONS

Larval bluefin tuna caught in the South Atlantic Bight in 1985 were in Gulf Stream water. Bluefin tuna larvae previously captured near Cape Hatteras were also in Gulf Stream water which meandered over the shelf edge. Larvae previously collected near Miami were primarily in the high velocity core of the Stream or in onshore meanders of the Stream. Therefore most bluefin tuna larvae off the southeastern U.S. were advected to the area, not spawned there. Although some unspent adults may spawn while migrating from the Gulf of Mexico to New England feeding grounds, only one of the larvae collected off the southeastern U.S. in 1985 had to have been spawned north of Miami based on its estimated age and rate of advection. The estimates of ages and advection do not falsify a hypothesis of local spawning with retention in recirculating currents, but the most likely conclusion considering all the evidence is that the South Atlantic Bight is not a major spawning area for western Atlantic bluefin tuna.

In addition, the habitat off the southeastern U.S. seems less favorable for bluefin tuna larvae because higher temperatures here than in the Gulf of Mexico would increase food requirements, and upwelling events over the shelf apparently do not lead to favorable food chains for larval tunas. Larvae may need to develop in retention areas outside the Loop Current in the Gulf of Mexico in order to synchronize their subsequent migration as schools of juveniles to nursery areas. These retention areas would be expected to vary in size and location with fluctuations in the Loop Current flow. The variations in amount of habitat for larvae could determine recruitment and thus affect the population dynamics of the bluefin tuna.

More research is needed to determine the survival rate of the larvae which are advected out of the Gulf of Mexico, to establish whether or not they recruit to the adult stock, to refine the definition of habitat for bluefin tuna larvae within the Gulf of Mexico, and to test if this habitat controls recruitment and population dynamics of the stock.

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Biomasses of Euphausiids and Smaller Zooplankton in the California Current—Geographic and Interannual Comparisons Relative to the Pacific Whiting, *Merluccius productus*, Fishery

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ABSTRACT: We examined data on size-fractionated zooplankton biomasses from the California Current in summer to 1) verify that euphausiid and smaller zooplankton biomasses varied in similar ways geographically and interannually, and 2) test for increase in euphausiid biomass after 1966, concurrent with initiation of a fishery on Pacific whiting (a major predator of euphausiids), and distinct from general, interannual changes. We accomplished purpose 1, but were unable to detect a significant effect attributable to the Pacific whiting fishery.

On the scale of years to decades and thousands of square kilometers, variability in the biomass of zooplankton, or of taxonomic categories within the zooplankton, can result from physical and chemical causes, from biotic interactions (especially in closed, manipulated systems such as lakes) or from some combination of these. In nonmanipulated systems, a plausible hypothesis is that variability results from a change in the physical processes influencing the area (the ultimate cause) plus ecological responses or readjustments of the populations present (the proximate cause). For the zooplankton of the open ocean, it is difficult to assess, by examination of case histories, the relative roles of physical and biological processes, because manipulation on the scales of interest is extremely difficult.

The California Current is known to vary interannually in transport and in physical properties—in aggregate, the Current's climate—the most extreme warming and decrease in southward flow being called El Niño (Wooster and Fluharty 1985). Correlated with (and in some sense probably caused by) these changes are variations in the biomass of zooplankton (Wickett 1967; Reid 1962). These changes are coherent through a large area—when zooplankton biomass is anomalously large or small in one area within the region, it tends to be large or small in all areas during the same year (Chelton et al. 1982). Further, several major taxonomic groups of zooplankton have similar interannual changes (Colebrook 1977).

By examining the timing of maximal zooplankton biomass relative to that of maximal southward flow, Roesler and Chelton (1987) concluded that off northern California interannual variations in biomass are caused by variations in direct advection of biomass from more northern regions (where biomass is high); off Baja California, variations in advection of nutrients from the north, translated via the food chain into zooplankton biomass with some lag, are more important.

Even in the presence of natural interannual variability, rapid development of a major commercial pelagic fishery is an anthropogenic manipulation which might cause detectable change in the biomass and/or composition of zooplankton. Pacific whiting, *Merluccius productus*, (also called Pacific hake) is one of the dominant fish in the California Current (Smith 1978). Euphausiids, especially *Euphausia pacifica* and *Thysanoessa spinifera*, make up > 70% of the weight of gut contents of whiting, especially fish <45 cm long, aged 3–4 years (Livingston 1983). *Euphausia pacifica* is a vertical migrator, at least much of the year (Brinton 1967; Brooks and Mullin 1983). *Thysanoessa spinifera* apparently remains in the upper 150 m at all times (Youngbluth 1976). Another prey of whiting, especially offshore, is the pelagic shrimp, *Sergestes similis*, (Alton and Nelson 1970), which has a nocturnal distribution similar to that of *E. pacifica* (Omori and Gluck 1979). Whiting guts are most full of food in the evening and early night (Livingston 1983), when the fish tend to be dispersed near the surface (Bailey et al. 1982).

In 1966 a foreign (later joint-venture) fishery, conducted from spring through fall, began removing considerable quantities of whiting in coastal regions off Washington, Oregon, and

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northern California (Nelson 1985). The commercial catch of pandalid shrimp in Oregon increased markedly at the time the Pacific whiting fishery began; from this coincidence, Bailey et al. (1982) and Francis (1983) suggested that the shrimp no longer eaten by whiting were available to fishermen, even though these commercial shrimp are only a minor portion of the whiting's diet. [Livingston and Bailey (1985) pointed out, however, that most of the increase in shrimp catch was due to increased fishing effort on shrimp rather than to increased catch per unit effort; hence it is not certain that the shrimp population has increased.] Nevertheless, the result and evidence of zooplanktivory summarized above stimulated an analogous question—whether the biomass of euphausiids increased in summer samples of zooplankton from the California Current off northern California in 1966–69, relative to summers of earlier years.

The trophic dynamics of the Pacific whiting, and the implications of the fishery, have been calculated from a simulation model by Francis (1983). His results indicated that the fishery may have reduced the (calculated) virgin whiting stock by about 21% without changing the annual production significantly because the production/biomass ratio increased. This conclusion implies that any indirect impact of the fishery on the whiting's food resources should be less than the change in the whiting's biomass. Francis also reasoned that the geographical distribution of food consumption by whiting would shift towards central California from northern California and Oregon.

Since the climate of the California Current is known to be correlated with interannual changes in the biomass of zooplankton, any change in euphausiid biomass must be scaled against the biomass of other zooplankton which would (presumably) be affected by climatic change but not directly affected by the removal of whiting. To test the assumption that the biomasses of euphausiids and smaller zooplankton respond similarly to climatic change, we reexamined data from the late 1950s, when there was a major El Niño.

We then determined the biomass of euphausiids and other pelagic shrimps (a major whiting food) relative to small zooplankton (not eaten by adult whiting) before and after the initiation of the fishery, and in a northern area closer to the fishery compared to further south, and then tested for significant differences. We also analyzed a published set of data from the California Current off cental Oregon (Pearcy 1976), since this was closer to the center of impact of the Pacific whiting fishery than were the samples available to us. Finally, we calculated whether, given the variances observed in the zooplankton samples we analyzed, we should have been able to detect a change in euphausiid biomass owing to partial removal of a major predator by the fishery.

METHODS

The California Cooperative Oceanic Fisheries Investigations (CalCOFI) yielded samples of zooplankton from the California Current from the mid-1940s to the present. Though the CalCOFI net is not a perfect sampler of euphausiids and other large, active, pelagic shrimp, samples taken at night (when most of these species migrate into surface waters) do contain euphausiids. From 1951 through 1968, the standard net was of mixed silk mesh—a large, forward portion of 0.55 mm and a small, rear portion of 0.25 mm—towed from the surface to a depth of 140 m. In 1969, the standard was changed to a net of uniform 0.505 mm nylon mesh, towed to 210 m (target depth). Though these procedures have been intercalibrated (Smith 1974; Hewitt 1980), care in interpretation of differences between pre-1969 and 1969 samples is necessary.

We divided nocturnal, summer (June–October) CalCOFI samples into the following space/time blocks or categories (Fig. 1): North of Monterey (CalCOFI line 70), 1960–65—41 samples (24 inshore); south of Dana Point (CalCOFI line 90), 1960–65—172 samples (103 inshore); north of Monterey, 1966–69—47 samples (25 inshore); and south of Dana Point, 1966–69—116 samples (73 inshore). "Inshore" samples, treated as a separate subset because of the inshore nature of the whiting fishery, thus constituted 53–63% of the samples in each block. Twenty-one other samples, in which no euphausiids were found, were excluded from statistical tests; at least two such samples occurred in each space/time block. The samples were from the following CalCOFI cruises (designated "aabb", where aa = year and bb = month): 6007, 6010, 6107, 6110, 6210, 6407, 6507, 6509 (southern area only), 6606, 6607, 6608 (southern area only), 6610, 6907, 6908, and 6910. We made analogous divisions into space/time blocks in the CalCOFI data set from the late 1950s and the set from Oregon.

Each sample consisted of formalin-preserved, unsorted zooplankton captured at one station by

a nocturnal tow. We fractionated each sample by sieving a subsample (≤ 0.5 of the sample) through a 4 mm screen, and counted and manually placed the euphausiids (and sergestids) retained on this mesh on a preweighed glass fiber filter. We then rinsed all or part of the same subsample sequentially through 1 mm and 0.5 mm meshes, using recirculating seawater, and then rinsed the plankton passing 1 mm but retained by 0.5 mm onto another preweighed glass fiber filter. We then rinsed both filters and their catches with 6% ammonium formate, dried them overnight at 50°–60°C, cooled them in a desiccator, and reweighed them. Blank filters (no zooplankton) were treated similarly. The dry weight of the sample, corrected for initial filter weight and any weight change of the blank filters, times the subsampling factor and divided by the volume of water filtered by the original net tow, is the biomass of "euphausiids" or of "small zooplankton" (that retained by the 0.5 mm mesh) for that station, and the weight of the euphausiids divided by their number is the dry weight per euphausiid.

With particular regard to the Pacific whiting fishery, which started in 1966 in the northern part of the California Current, and the expectation that biomass of whiting food might increase, we tested the following null hypotheses (stated in the "one-tailed" forms appropriate for our expectations).

H_{01}—Absolute biomass of euphausiids in the northern area was not greater from 1966 onward than that before 1966.

H_{02}—The ratio of biomasses (euphausiids/small zooplankton) in the northern area from 1966 onwards was not greater than a) this ratio before 1966, or b) that in the southern area. [The small zooplankton biomass is used to correct for the expected north-to-south differences, overall changes in the biomass of zooplankton, or change in sampling techniques, throughout the California Current for reasons other than the whiting fishery.]

H_{03}—The dry weight per euphausiid in the northern area was not greater from 1966 onward than before 1966.

Hypothesis H_{02}a, for example, was examined by a one-tailed rank sum (Mann-Whitney U) test of whether the median of all ratios at northern stations before 1966 was statistically indistinguishable from the median for all such stations beginning in 1966. The alternative which would be consistent with an effect of the whiting fishery would be, pre-1966 median <1966-and-later median. In some cases, analogous *t*-tests were also performed on data normalized by log-transformation to determine whether transformed means differed. In this approach, all stations within one block of geography and time are treated as equally valid estimates of the overall median, independent of location of the stations within the block.

There are significant inshore/offshore gradients in biomass (see below), and comparisons between years or between areas could be confounded by differences between groups being compared in the inshore/offshore locations of usable samples. We took several precautions to prevent this; first, we tested for such gradients in our own samples by comparing medians from inshore and offshore subsets of stations by rank sum tests. We also tested hypotheses H_{01}–H_{03} using only the inshore subsets of the stations (Fig. 1); this was done partly because the fishery for whiting is generally conducted in areas shallower than 500 m.

We tested analogously data from a transect off Oregon which was repeatedly sampled from 1962 to 1967 (see below).

Hypotheses H_{01} and H_{02}a were tested further by another approach which acknowledges that within each major space/time block, stations may differ systematically because of geography (e.g., an inshore/offshore gradient), so that the identity of each station should be retained in the test. The data from each northern California station which was sampled at least thrice before 1966 or in 1966–69, and at least once during the contrasting period, were ranked separately as for a rank sum test, but the summed ranks were then combined for testing against the expectation from the null hypotheses. There were 7 stations used in this test, and 21 data points from each period.

Falsification of these hypotheses implies that there was a significant increase in euphausiid biomass (and/or individual size) coincident with the whiting fishery and that this increase was unlikely to be caused by other factors affecting zooplankton in the whole California Current, including those types on which adult whiting do not feed.

In order to validate the assumption which underlies H_{02}—that small zooplankton and euphausiid biomasses vary in parallel in response to the California Current's climate—we

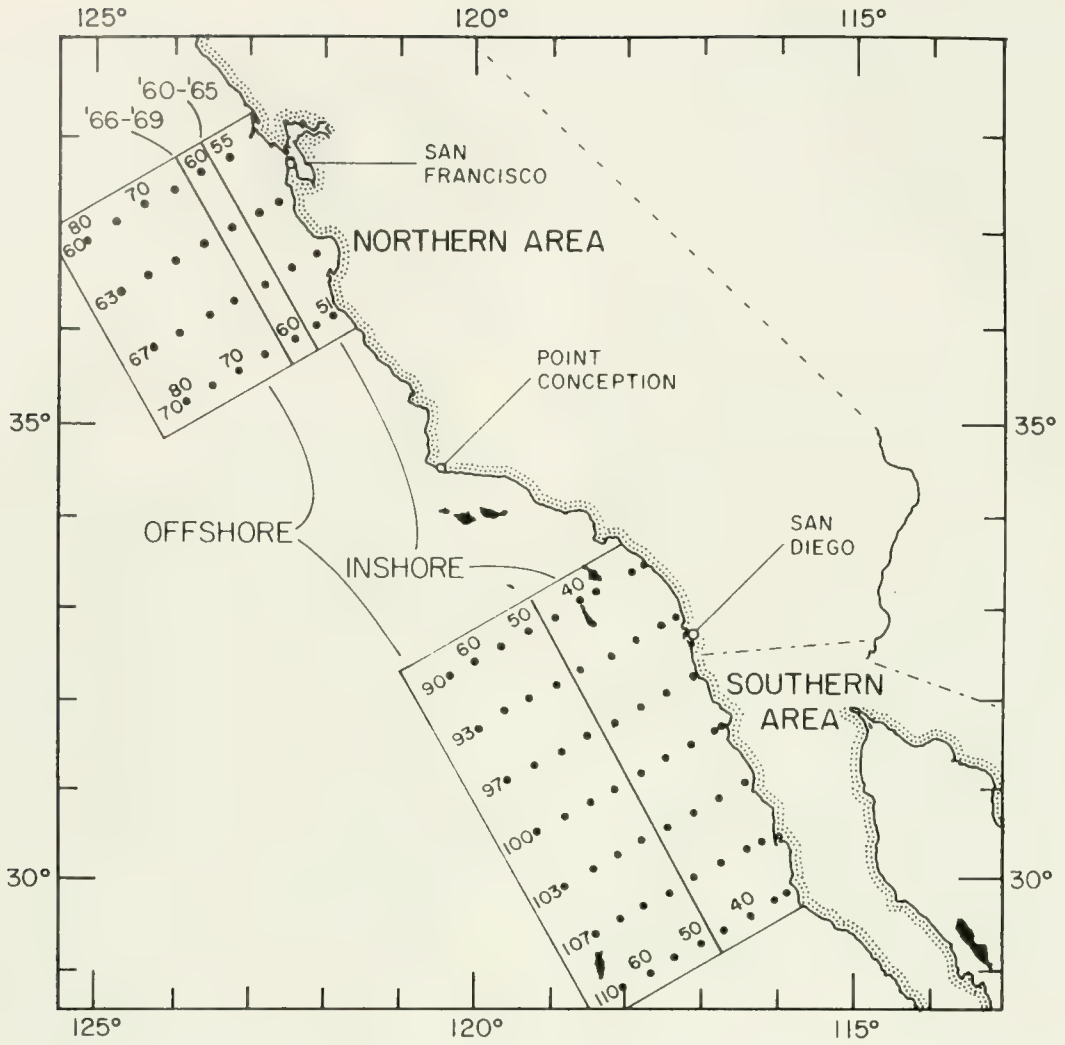

FIGURE 1.—Northern and southern areas, and CalCOFI transect line and station numbers. Each area is divided into "inshore" and "offshore" subsets of stations: the dividing line used in the northern area for 1960–65 was closer to shore than that for 1966–69 because the distribution of samples differed. The same areas were used for data from the 1950s, with same inshore/offshore divisions as in 1960–65.

used published data from 1958 and 1959, during which there was a major El Niño, compared with 1955–57. Zooplankton from the California Current during these years had been visually classified into 17 categories, and wet weight biomasses were assigned to each (Isaacs et al. 1969). We examined "euphausiid" and "copepod" categories of this data set (assuming from our visual examination that the "copepods" were most similar to our "small zooplankton" category), selecting those stations which were nocturnal and within the areas defined in Figure 1 during April, July, and October, and separating 1955–57 from 1958–59. This resulted in 21 northern, 1955–57 stations (13 of which were inshore); 49 northern, 1958–59 stations (30 inshore); 118 southern, 1955–57 stations (72 inshore); and 110 southern, 1958–59 stations (63 inshore). We then performed statistical tests analogous to those described above to test hypotheses concerning similarity of geographic and temporal variation of euphausiid and copepod biomasses, and constancy of their ratio.

RESULTS

Interannual Variation of Euphausiids and Copepods, 1955–59

Colebrook (1977) demonstrated by multivariate analysis overall north-to-south and inshore-to-offshore trends in the annual mean values of zooplankton biomass in the California Current. He found that the biomasses of euphausiids and

copepods particularly decreased moving offshore. The biomasses of both categories were larger in 1955 and 1956 (pre-El Niño years) than in 1958 and 1959 (El Niño years; see also Chelton et al. 1982). This suggests that biomasses of euphausiids and of the smaller copepods respond similarly to interannual climatic or environmental variation.

Our results, which are summarized in Figure 2, were

1) Biomasses of euphausiids and copepods were significantly less in the southern area than in the northern area, both before (1955–57) and during (1958–59) the El Niño, in agreement with Colebrook's (1977) conclusions, and the ratio of euphausiid to copepod biomasses did not change significantly. Analysis of data from only the inshore subareas yielded the same results, except that the euphausiid biomass did not differ significantly between northern and southern inshore areas during 1958–59.
2) Biomasses of euphausiids and copepods were significantly less during El Niño than before it, both in the complete areas and in the inshore portions (also agreeing with Colebrook's result), and the euphausiid/copepod biomass ratio did not change significantly.
3) Neither the euphausiid nor the copepod biomasses were significantly different between inshore and offshore subareas, nor were the ratios significantly different (comparison not shown in Figure 2); this result differs from Colebrook's conclusion.

Overall, we conclude that it is reasonable to use the biomass of small zooplankton to correct or scale the biomass of euphausiids for effects of geography or interannual climatic variation in order to test for changes due to factors specific to the euphausiids.

Interannual Variation in 1960–69 off California

Averaged over the entire decade, there were significantly lower biomasses of euphausiids and of small zooplankton offshore than inshore, both in the southern area by itself and in the combined areas (unlike our result for 1955–59). Thus, for testing hypotheses (such as H_{01}) concerning biomasses, the inshore/offshore distribution of samples should be similar in the sets being compared (as was true in our case). We were unable, however, to reject the null hypothesis that the median ratio of biomasses in the offshore subset of stations equalled the median

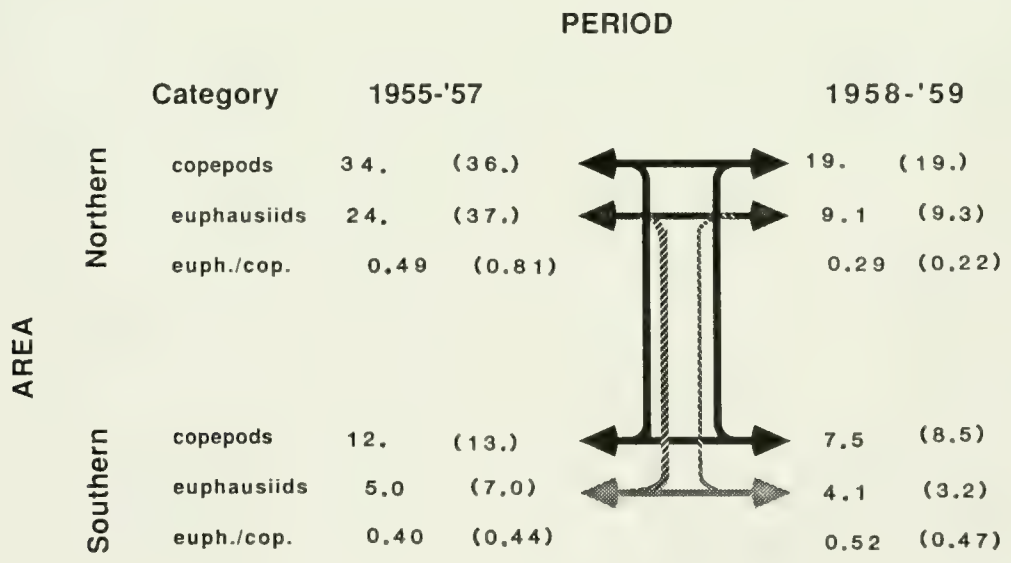

FIGURE 2.—Overall and (inshore subset) medians for each space/time block in the 1950s, for wet weight biomasses ($mg \cdot m^{-3}$) of copepods and euphausiids, and for the ratios at individual stations. Arrows connect medians which differed significantly ($P < 0.05$ for H_0 = no difference); a thick arrow indicates that the comparable medians of the inshore subsets of data also differed significantly. All comparisons were "vertical" or "horizontal"; no "oblique" comparisons were tested (e.g., no comparison between northern, 1960–65, and southern, 1966–69).

ratio at the inshore stations, either in the northern and southern areas separately or in the combined areas. Since we could not detect persistent gradients by this test (nor by analogous *t*-tests), we concluded that differences in the inshore/offshore placement of samples between two groups should not preclude the testing of hypothesis H_{02}, which concerns ratios.

In comparisons between periods or between areas (Fig. 3), the most significant difference was the greater biomass of the "small zooplankton" in the north in 1966–69 than the northern, 1960–65 or the southern, 1966–69 biomasses. These differences were significant ($P < 0.05$) even when the inshore subsets of data only were considered. Probably as a result of this, the ratio of euphausiid to small zooplankton biomasses was significantly lower in the northern, 1966–69 data set than elsewhere. This difference was also significant by *t*-test.

The biomass of small zooplankton was significantly greater in the northern than in the southern area in both periods, in fact (as in 1955–59). The null hypothesis that the biomass of euphausiids was the same in all sets of data could not be rejected. Nor did the weight per euphausiid in the northern area change.

These results were supported by the comparison of biomasses at specific northern stations which had been sampled several times. The biomass of small zooplankton was greater, and the euphausiid/small zooplankton ratio less, in 1966–69 than in 1960–65 ($0.05 < P < 0.1$ by two-tailed test in both cases), while the biomasses of euphausiids did not differ ($P > 0.1$).

The significant increase in median biomass of small zooplankton in 1966–69, relative to 1960–65, could have been due to the inclusion of data from 1969, when samples were taken differently (see Methods) if the different method itself resulted in increased catch. However, Smith (1974) reported that the method used in 1969 resulted in a *smaller* biomass (per unit volume filtered) than did the pre-1969 method. In our data, the biomass of small zooplankton was greater, and the euphausiid/small zooplankton ratio less, in 1966 than in 1969 (rank sum tests). Hence, the change in sampling in 1969 could hardly have been responsible, in itself, for the elevated biomass of small zooplankton in 1966–69 relative to the earlier years.

Thus, euphausiid biomass could not be shown to increase coincident with the onset of the whiting fishery, either in absolute units or relative to the small zooplankton. None of the null hypotheses relating to absence of change of euphausiids in the northern area at the time of the whiting fishery could be rejected, and in fact the ratio of

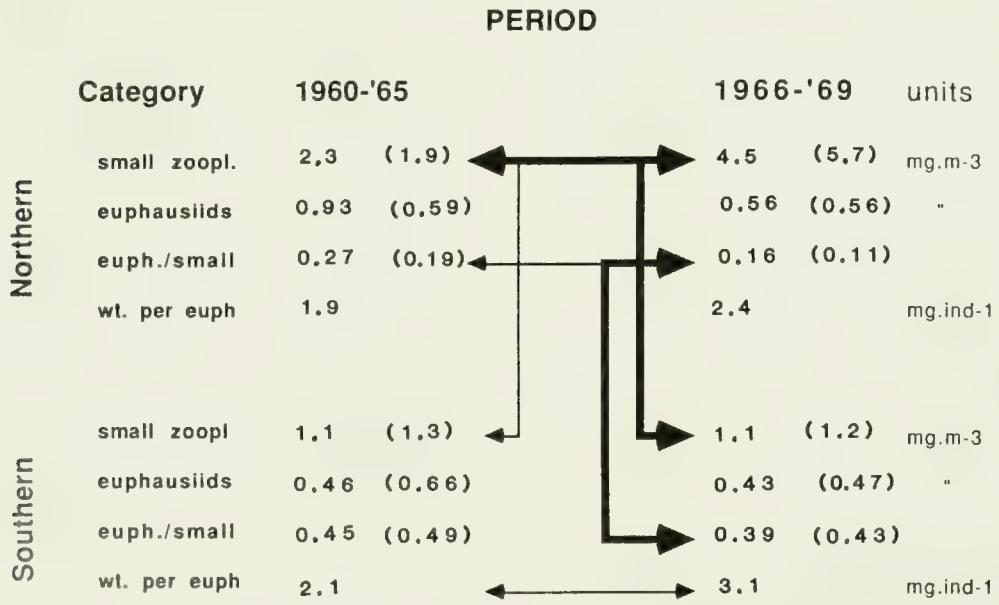

FIGURE 3.—Overall and (inshore subset) medians for each space/time block in the 1960s, for dry weight biomasses of small zooplankton and euphausiids, their ratios, and the dry weights per euphausiid. Arrows connect medians which differed significantly ($P < 0.05$ for H_0 = no difference); a thick arrow indicates that the comparable medians of the inshore subsets of data also differed significantly. All comparisons were "vertical" or "horizontal"; no "oblique" comparisons were tested.

euphausiid to small zooplankton biomass differed significantly in the direction opposite to that predicted.

Interannual Variation in 1962–67 off Oregon

We also examined similar hypotheses using data provided by W. G. Pearcy (see Pearcy 1976) for a repeatedly sampled transect from the Oregon coast seaward to 530 km, since this region is closer to the geographic center of the Pacific whiting fishery than was our California, northern area. The data set includes 89 values for dry weight biomasses of euphausiids and copepods from nocturnal samples from April to October 1962–67. By analogy to our treatment of California data, we defined inshore as the innermost 100 km, and offshore as the remainder of the transect; we therefore divided this set into subsets, 1962–65 (56 total samples, 34 inshore) and 1966–67 (33 samples, 20 inshore).

To compare results from this Oregon transect to one transect within the "southern" area, we chose CalCOFI line 93 (see Figure 1), and subdivided samples from it into similar subsets: 1960–65 (33 samples, 17 inshore) and 1966–69 (23 samples, 14 inshore). The direct comparison of biomass off Oregon to that on line 93 means little, since the methods differed (for instance, we measured "small zooplankton" and Pearcy measured copepods), but we could compare the patterns of variation shown on the two transects.

On line 93, biomass of euphausiids was significantly less offshore than inshore (as was true for the entire southern area), and the biomass of small zooplankton tended similarly, though the difference was nonsignificant. Neither the small zooplankton nor the euphausiid biomass, nor their ratio, differed between 1960–65 and 1966–69—conclusions which also characterized the entire southern area (Fig. 3). The Oregon transect revealed a similar spatial pattern (significant decreases of biomass offshore for both copepods and euphausiids) and a similar lack of temporal change (no significant changes for the entire transect, or its inshore portion, in copepod biomass, euphausiid biomass, or their ratio) between 1962–65 and 1966–67.

Therefore, the patterns off Oregon were very similar to those off southern California, and failed to indicate a change in the biomass of euphausiids concurrent with the whiting fishery off Oregon.

Expected Response of Euphausiid Biomass to the Pacific Whiting Fishery

Detection of a change in the biomass of euphausiids which could be caused by the start of the whiting fishery depends on 1) the magnitude of the change in the predatory impact on euphausiids due to change in the stock of whiting, 2) the rapidity with which the community readjusts to such changes, and 3) the variability among the available samples in which change is to be detected. Francis (1983) calculated the food consumption by the virgin and exploited whiting stocks in several standard regions of the North American west coast; these estimates can be applied to the areas we sampled by making various assumptions about the more detailed geography of the effect of the fishery on the whiting stock. The variances of the groups of samples we analyzed give an estimate of the "noise" against which this "signal" must be detected, and, as discussed above, we can use the biomasses of copepods to correct for long-term variability.

Since we were unable to detect a change in biomass of euphausiids attributable to the Pacific whiting fishery, we did a simple calculation to determine how many samples, with the same variances as the samples we did analyze, we would have had to analyze to detect an expected change at the 0.05 probability level, if 1) only the change in whiting stock affected the biomass of euphausiids, or 2) if changes in the biomass of small zooplankton were used to normalize the euphausiid biomass for nonfishery effects (i.e., using a simplified euphausiid/small zooplankton biomass ratio).

First, we assumed that the biomass of euphausiids was in equilibrium before the start of the fishery in 1966, such that the sum of mortality and growth was zero and immigration equalled emigration, and that subsequently a biomass of euphausiids simply accumulated, proportional to the decrease in whiting predation, without change of the population parameters. We averaged the biomasses of euphausiids from all samples in a given area from 1960 to 1965, and then calculated the expected biomass two years after the start of the fishery from the change in consumption by whiting in that area, using the estimates of Francis (1983) corrected for the fraction contributed by euphausiids to whiting gut contents (Alton and Nelson 1970; Livingston 1983; Rexstad and Pikitch 1986), for the dry/wet weight ratio, and for the volume represented by

that area. Thus, we calculated an "expected" biomass of euphausiids at the end of 1967, E_a, from the mean biomass before the start of the fishery, E_b. The maximum expected increase was 50% in the northern California inshore area.

To test for significant differences by two-sample t-test between the means of nonnormal data sets, we would transform to logarithms and verify that this normalized the data (as was true for our data sets) before performing the test. If the means of the log-transformed data are E_a^* and E_b^*, the critical value for the t-test, for given numbers of samples, then indicates how much E_a^* must exceed E_b^* for the difference to be significant, given the variance around E_a^* and E_b^*, and thus defines a critical ratio, $(E_a/E_b)_{cr}$, for nontransformed data (see Appendix A). Conversely, we can ask how many samples would need to be analyzed from a particular area such that $E_a/E_b > (E_a/E_b)_{cr}$.

We did this calculation for the entire areas, and the inshore portions, of northern California and Oregon. In order to detect significance, we would have had to analyze between 80 and 1,600 samples for each block of time within an area, depending on the area. Therefore, the numbers of samples we analyzed, and the data set from Oregon, were insufficient to detect the simplest expectation.

Next, to normalize the euphausiid biomasses, we multiplied the ratio, E_a/E_b, by the comparable ratio of means of observed, log-transformed, small zooplankton or copepod biomasses to obtain a ratio of euphausiid biomasses, $(E_a/E_b)_{corr}$, corrected for the environmental or climatic change reflected in these biomasses, which increased significantly off northern California (Fig. 3), and compared $(E_a/E_b)_{corr}$ to $(E_a/E_b)_{cr}$. In the Oregon data set, $(E_a/E_b)_{corr} < (E_a/E_b)_{cr}$, the expected change could not have been detected with the available data. In both inshore and total areas of northern California, however, $(E_a/E_b)_{corr} > (E_a/E_b)_{cr}$ meaning that a t-test should have been able to detect a significant increase in biomasses of euphausiids in northern California due to the combined effect of environmental change and the whiting fishery, if only these two factors operated in the most simple, additive fashion.

DISCUSSION

Our results, like those of Colebrook (1977), show considerable similarity in the large-scale geographic and interannual variations in biomass of euphausiids (at least those caught by the CalCOFI net at night) and smaller zooplankton. It is also clear that the impact of a climatic event like El Niño greatly exceeds, on these scales, any effect of the whiting fishery.

The failure to find greater biomasses of whiting prey after the beginning of the fishery in the Californian area north of Monterey, or off central Oregon, could result from undersampling, from a mismatch between the effect of the fishery on the whiting population and the zooplankton sampled by plankton nets, and/or from the complexity of the ecological relations affecting euphausiid biomass.

"Undersampling" means that variability within each space/time group of samples is so great that we cannot statistically detect differences between groups even though differences actually exist which would be detected if more samples were available. As we have shown, the change in euphausiid biomass calculated from a model of the biomass and food consumption of exploited and virgin Pacific whiting stocks could not have been detected statistically without at least three times the number of samples we had. Further, the actual biomasses of euphausiids off both northern California and Oregon tended to decrease, as did the ratios of euphausiid to small zooplankton (or copepod) biomasses. Therefore, we doubt that simply analyzing more samples of the same kind (i.e., from the same sampling pattern, using the same gear) would demonstrate the anticipated increase in the biomass of euphausiids.

Because CalCOFI stations north of San Francisco were not sampled after April of 1960 during that decade and because the whiting fishery was centered off Oregon and Washington, the samples in our northern California area (Fig. 1) were too far south to be ideal for this analysis, as well as extending too far offshore. The transect off Oregon was better placed latitudinally, but the number of samples in the inshore zone (where the Pacific whiting fishery was conducted) was rather small. Therefore, our effort to increase the number of samples to be analyzed resulted in inclusion of areas outside that where the predators had been reduced by the fishery; we were, in a sense, trying to detect advection or diffusion of the effect into a larger area.

Ecological complexity may have buffered the response to a reduction of a predator such as whiting in ways that do not ameliorate climatic effects. The relatively simple outcome—that euphausiids became absolutely or relatively

more abundant following the initiation of the fishery—could have been overshadowed by, e.g., 1) replacement of whiting by the increase of some other species of predator on euphausiids, even a species which is also prey for large whiting (Livingston 1983); 2) differential removal of large whiting by the fishery, leaving smaller whiting whose preference for euphausiids as food exceeded that of the larger fish, so that predation pressure did not decrease dramatically because of altered age structure of the whiting population; or 3) replacement of predator-limitation by food-limitation of euphausiid biomass.

We tried to minimize the effect of response 1) by restricting the post-1965 analysis to the years immediately following the initiation of the fishery, on the theory that this might have represented a period of abundant euphausiids before the ecosystem returned to a new equilibrium through the increase of a new, major zooplanktivore. Unfortunately CalCOFI coverage of the northern California Current in the summers of 1967 and 1968 was very small.

Response 3) is possible (indeed, euphausiid biomass may never have been limited by Pacific whiting's predation), but the increase in biomass of small zooplankton in the northern California area in 1966–69 (Fig. 3) suggests a food supply which could have supported an increased biomass of euphausiids—an increase which was not realized.

In considering the possible responses of the zooplanktonic community to the Pacific whiting fishery, it is worth remembering that there have been natural fluctuations in the whiting population as great as those caused by fishing. Oceanographic variation in the whiting's spawning area is important, higher temperatures being associated with greater, and more variable, recruitment (Swartzman et al. 1983; Bailey and Francis 1985). Judging from scales collected in an anoxic basin, whiting was much more abundant off Southern California in the 30 years around 1900 than in recent years (Soutar and Isaacs 1974). Such fluctuations in the stock of whiting are therefore only a manifestation or symptom of more general environmental variation in the California Current.

Overall, our results indicate that a major environmental perturbation, such as El Niño, acts on the California Current's ecosystem as a whole (though the mechanism of action may differ geographically; Roesler and Chelton 1987) and modifies the components we studied in similar ways. The system seems to adjust to more local, specific modifications, such as anthropogenic changes in biomass and age structure of one predator, so that widespread effects on planktonic prey populations are difficult to detect.

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APPENDIX A

Caution must be used when performing a logarithmic (ln) transformation [$y_i = \ln(x_i)$] on data (x_i) belonging to a nonnormal distribution. The resulting mean of the log-transformed data

$$\bar{y} = \frac{\sum_{i=1}^{n} \ln(x_i)}{n}$$

is equal to the logarithm of the geometric mean of the untransformed data

$$\bar{y} = \ln\left(\sqrt[n]{\prod_{i=1}^{n} x_i}\right).$$

Since the geometric mean is always less than the arithmetic mean (Zar 1984), the antilog of the mean of the log-transformed data must be corrected before it can be used as an unbiased estimation of the arithmetic mean of the untransformed data.

Bagenal (1955) showed a relationship between the means of transformed ($\bar{y}$) and untransformed ($\bar{x}$) data, which is valid when the transformed data belong to a normal distribution, with mean = $\bar{y}$ and variance = σ_y^2.

$$\bar{x} = e^{\bar{y} + \frac{1}{2}\sigma_y^2} \tag{1}$$

and

$$\bar{y} = \ln(\bar{x}) - \frac{1}{2}\sigma_y^2 \tag{2}$$

We applied this relation to our calculations of the critical differences between the means of log-transformed biomasses after and before the beginning of the fishery. The data had to be log-transformed in order to perform the two-sample t-test, since this assumes that the distributions underlying the two samples are normal.

The critical differences were so calculated, from the two-sample t-test formula:

$$E_a^* - E_b^* = t' \, s_p \sqrt{\frac{n_a + n_b}{n_a \, n_b}} \tag{3}$$

where E_a^*, E_b^* are, respectively, the means of the log-transformed biomasses after and before the beginning of the fishery, equal to $\bar{y}$ in Equation (2),

t' is the critical t-value at $\alpha = 0.05$,

s_p is the pooled variance for the two samples, and

n_a,n_b are, respectively, the numbers of samples after and before the beginning of the fishery.

These differences were then related to the means of untransformed data by applying Equation (2):

$$E_a^* - E_b^* = \ln(E_a) - 0.5\, s_p^2 - \ln(E_b) + 0.5\, s_p^2 = \ln\left(\frac{E_a}{E_b}\right) \tag{4}$$

where $E_{a,b}$ indicate arithmetic mean of untransformed biomasses, analogous to $\bar{x}$ in Equation (1).

And therefore, from Equations (3) and (4), a critical ratio was defined:

$$\left(\frac{E_a}{E_b}\right) \text{cr} = e^{\left(t' s_p \sqrt{\frac{n_a + n_b}{n_a n_b}}\right)} \tag{5}$$

which is the minimum ratio necessary to reject the null hypothesis.

Note, however, that the correcting factors ($0.5\ s_p^2$) cancel each other only when using a t-test with pooled s^2, i.e., when assuming the two samples belong to the same distribution.

Growth During the Larval and Juvenile Stages of the Northern Anchovy, *Engraulis mordax*, in the California Current During 1980–84

John L. Butler

ABSTRACT: Increment widths and back-calculated growth rates for northern anchovy, *Engraulis mordax*, did not differ during the years 1980–84. This evidence of stable larval growth rates does not support the theory that it is the variation in larval growth rates that directly affects the magnitude of recruitment. Furthermore, since growth rates remained stable, even though zooplankton volumes in 1983 were well below the long-term mean, it follows that surviving post-first-feeding larval anchovies may not be food limited.

The size of juvenile northern anchovy was reduced during the 1982–83 El Niño "phenomenon" in the California Current. Mean lengths of anchovy juveniles collected in the fall were greatest in 1980, least in 1982, and intermediate in 1981, 1982, and 1984. Growth rates back calculated from otolith increment widths did not differ significantly between the 1980 and 1983 cohort, until 100 days after first feeding. Reduced growth after 100 days largely determined the smaller size of 1983 anchovy juveniles. Condition factor was also reduced in the 1983 cohort. The 1982 cohort was not greatly affected, because El Niño did not have a pronounced effect off the North American coast until well after the 1982 northern anchovy spawning season.

Through the years, the overall abundance of many pelagic fishes varies with the strength of individual year class; changes in mortality rates early in life (Hjort 1914, 1926), rather than parent stock size, may determine the size of individual year classes. Considerable controversy, however, surrounds details of the exact stage and mechanism through which changes in individual year-class strength occur.

The co-occurrence of fish larvae and their food is a mechanism that has been proposed to explain variations in year-class strength (Hjort 1914, 1926). Lasker (1978) has shown that food availability may affect survival of first-feeding northern anchovy, *Engraulis mordax*, larvae in the sea. Food availability may not affect the survival beyond the first-feeding stage; however, Methot (1981) found that early larval anchovy growth rates in the sea were the same as those of well-fed, laboratory-reared larvae. Survival through the larval stage does not determine the magnitude of the northern anchovy recruitment (Peterman and Bradford 1986; Peterman et al. 1988). Thus food availability for larvae may not determine the year-class strength and whether food availability affects juvenile survival are yet to be investigated.

A simulation model of the northern anchovy population indicates that the growth rate of late larvae and early juveniles may affect the magnitude of recruitment (Smith 1985). If mortality rates in the marine environment are size-specific, as predicted by Peterson and Wroblewski (1984), and if growth rates determine the duration of the most vulnerable stages, reduced growth should adversely affect survival. The extent to which growth rates of late larvae and juveniles vary is unknown.

The growth rate of juveniles also affects adult size. Off southern Baja California, the adult size of northern anchovy is entirely determined by juvenile growth, because these fish show no growth after 18 months (Parrish et al. 1985). Analysis of the regional patterns of growth of northern anchovy shows that the average length of fish at a given age increases from south to north. The length at 18 months ranges from 101.1 mm off southern Baja California to 126.6 mm off central California (Parrish et al. 1985).

Because batch fecundity is a function of body size in broadcast spawners, the juvenile and adult growth rates determine the reproductive capacity over the adult lifespan. Competition among juveniles for resources affects adult fertility in other species (Prout and McChesney 1985), and, if growth of juvenile pelagic fishes is food limited, competition among juveniles may

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be a mechanism of density-dependent compensation.

Growth rates of larval and juvenile anchovy during El Niño periods are of particular interest, because the growth rates during an environmental perturbation may reveal details of the processes of growth and survival during normal conditions. During the 1982–83 El Niño event off California, temperatures were elevated (Lynn 1983; Simpson 1983) and zooplankton density was reduced in 1983 (McGowan 1985). If planktivorous fish compete for food, competition should be highest when zooplankton abundance is lowest. Comparison of growth rates throughout the larval and juvenile stages during periods of low and high food abundance may show the size range at which the larval or the juvenile stage is most important. In this paper I examine the interannual variability in growth rates of anchovy larvae and juveniles during periods of low and high food abundance.

METHODS

Samples of juveniles from the central population of northern anchovy were obtained from midwater trawl hauls taken in 1980–84 by the Sea Survey Program of the California Department of Fish and Game. Annual cruises to monitor the strength of the incoming year class of northern anchovy have been conducted during September and October since 1976; Mais (1974) has described the gear and sampling procedures. The surveys extended along the Pacific coast from central Baja California to Point Conception, CA, with the exception of 1982, when the southern limit was the U.S.-Mexican border. Trawl hauls were taken nearshore inside of a 75 fm contour where young of the year are most abundant during the fall (Parrish et al. 1985).

Twenty five juvenile northern anchovy were randomly taken from each positive trawl haul and frozen for age determination. A subsample of 200 juvenile anchovy was randomly taken from the 800 to 1,000 fish collected on each survey for analysis of growth rate using daily increments in the otoliths. Fish were measured from the tip of the snout to the posterior edge of the hypural plate (standard length), and otoliths were removed and mounted on microscope slides using Eukitt[1] mounting medium.

Growth rates and ages of juvenile northern anchovy were determined by counting and measuring daily increments in the otoliths (Methot 1981). The increment widths were measured and recorded along a transect from the focus to the posterior margin of the otolith (otolith radius), using a video-coordinate digitizer connected to a microcomputer. The otoliths were progressively polished between readings, using 15 and 0.3 μ lapping film, to reveal increments along the entire transect. Data from different areas of the otolith were collected as the increments became visible. During each reading groups of 10 or less (typically five) increments were counted and measured. The number of increments measured was reduced if width varied among increments.

ANALYSIS AND RESULTS

Data from both otoliths and several replicate transects per otolith were combined to calculate age and otolith increment widths (Methot 1981). Mean increment width was calculated at each point along the radius from the focus to the posterior margin of the otolith. In some cases, it was impossible to obtain measurements of all increment widths in the otoliths. In these cases, increment widths were interpolated using linear approximation (see Methot 1983 for details). Data for increment widths and age estimates were not used if more than 5% of age was calculated from interpolated increments.

A direct comparison of the average size of recruits from year to year is inappropriate because their ages may differ from year to year owing to differences in the dates of spawning (Methot 1983) or to dates of collection. To eliminate this bias, the dates of hatching were determined from the dates of sampling and ages, and fish were grouped by year and month of hatching.

Interannual and seasonal differences in length were tested, using an analysis of covariance (Bartlett et al. 1984) with age as the covariate. This analysis adjusted the mean length to the grand mean age of 208 days, approximately the time elapsed from the peak of spawning to the date of capture. Since the relation of length to age is typically nonlinear, some error is introduced using a linear adjustment. The difference in dates of sampling is, however, only about one month and the relation of size to age is approximately linear from two to six months.

Analysis of covariance of these data indicates parallel lines with differences in means (Case 2c

[1]Reference to tradenames does not imply endorsement by the National Marine Fisheries Service, NOAA.

in Bartlett et al. 1984). Thus, comparison of lengths adjusted by age between years of fish hatched during the same calendar month is reliable. Comparison of lengths of fish hatched at the extremes of the same spawning season may be less reliable than between-year comparisons. Fish hatched in January are four months older than fish hatched in May, and linear extrapolation to a common age may introduce error. However, since growth is decelerating, linear extrapolation overestimates mean lengths of fish hatched at the extremes of the spawning season. The fact that lengths of fish hatched in January and May in all years, except 1983, are less than lengths of fish hatched in March indicates that the error is not great.

The allometric relations of length and weight to otolith radius were estimated using nonlinear regression. These relations were used to back-calculate age-specific size and growth rates for individual fish; not all fish were weighed in 1980 and 1981, and data were pooled from 1980 to 1982 to determine the allometric relations of both length and weight to otolith radius. Individual relations were determined for 1983 and 1984.

The growth rates in length and in weight were determined from increment widths and the first derivative of the empirical relationship of fish size and otolith radius. The condition factor (dry weight/length cubed) was significantly less in anchovy juveniles collected in 1983 than in anchovy juveniles collected in 1980–82. Therefore, the algorithm to convert otolith increment size to growth in dry weight differed among years. The equation used to calculate growth in length was

$$\Delta L/\Delta t = (\Delta R/\Delta t)(\Delta L/\Delta R); \qquad (1)$$

where $\Delta R/\Delta t$ is rate of change of the width of the daily increments, and $\Delta L/\Delta R$ is the slope of the observed relationship of fish length and otolith radius.

The variance of the product (Y) of two variables (X, Z) is given by

$$\mathrm{Var}(Y) = Z^2\mathrm{Var}(X) + X^2\mathrm{Var}(Z) + 2XZ\,\mathrm{Covar}(XZ) \qquad (2)$$

if the variables are not independent (Goodman 1960). The estimate of the variance of $\Delta R/\Delta t$ was the variance of the measurement of increment width of the fish in each group. If the length, radius relation was linear, the variance of $\Delta L/\Delta R$ was estimated from $S^2_{Y|X}$, the variance of the slope of the regression of length on otolith radius. If the relation of length to radius was nonlinear, as was often the case, the variance of $\Delta L/\Delta R$ was estimated by partial derivatives. The variance of $\Delta W/\Delta R$ was not calculated; the complex derivative may not be a good estimate of the true variance.

The author tested the assumption that the covariance was equal to zero by comparing the slopes of the relations of juvenile fish length and otolith radius for 70–100 mm, slow- and fast-growing fish collected in October 1984 that were $\geq$ 1 year old. The slope was 0.0419 for anchovy older than one year and 0.0314 for fish younger than one year old. These slopes were not significantly different ($P > 0.10$, ANCOVA). Consequently confidence intervals around back-calculated growth rates were calculated ignoring the third term in Equation (1).

Lengths of anchovies were significantly different between months and years ($P < 0.01$, ANCOVA). Within a spawning season, fish hatched during February, March, and April grew faster than fish hatched in January or May (Fig. 1), although this was not evident for the 1983 or 1984 data. The mean of five fish in January 1982 was not different from that of the April 1982 sample. The adjusted lengths of juveniles collected from the 1983 year class where less than the adjusted lengths of any of those from 1980–82 for all months but May (Fig. 1, Table 1). The adjusted lengths of juveniles from

TABLE 1.—Mean lengths at capture of juvenile northern anchovy hatched in various months of 1980–84, adjusted to a common age of 208 days. SE and *N* stand for standard error and number of fish, respectively.

	Month of Hatching				
Year	Jan.	Feb.	Mar.	Apr.	May
1980	71.4	78.7	84.6	83.6	72.3
SE	3.6	1.6	1.0	1.6	
N	7	30	104	33	2
1981	77.0	79.9	83.5	82.7	79.7
SE	2.2	2.2	1.2	1.5	2.4
N	21	29	42	35	16
1982	81.1	85.79	84.1	81.0	78.9
SE	4.5	1.3	1.1	1.2	1.6
N	2	32	70	53	29
1983	70.0	71.4	71.5	70.8	73.7
SE	2.6	2.1	0.9	0.9	2.7
N	9	17	99	45	8
1984	74.8	77.0	76.0	76.8	75.6
SE	1.5	1.3	1.3	1.9	1.5
N	39	53	42	22	17

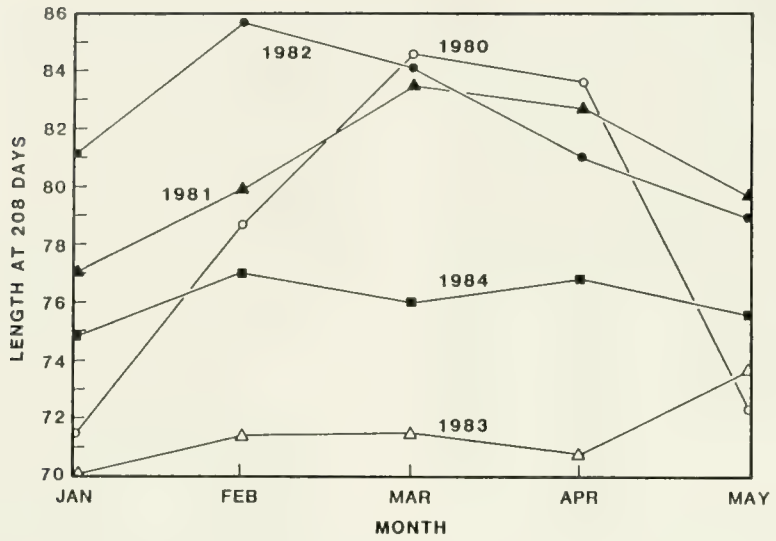

FIGURE 1.—Mean lengths adjusted for age of northern anchovy spawned in 1980–84. For each year, fish are grouped by back-calculated date of hatching, and length at capture is adjusted to mean age of 208 days.

1984 were intermediate between those of 1980–82 and 1983.

Fish hatched during 1983 did not grow more slowly throughout the entire larval and juvenile stage than during other years. Otolith increment widths from 104 juveniles hatched in March 1980 were compared with otolith increment widths from 99 juveniles hatched in March 1983 (Fig. 2). In fish smaller than 40 mm in length, increment width was not different. Above 40 mm, the otolith increment widths were smaller in the 1983 sample than in the 1980 sample ($P < 0.01$); the 95% confidence limits for the two cohorts did not overlap. These results show that the difference in lengths of the two cohorts indicated by the analysis of covariance is largely due to difference in growth rate after a size of 40 mm, rather than to a reduction of growth throughout life.

Back-calculated lengths and growth rates of 1980 northern anchovy juveniles were greater

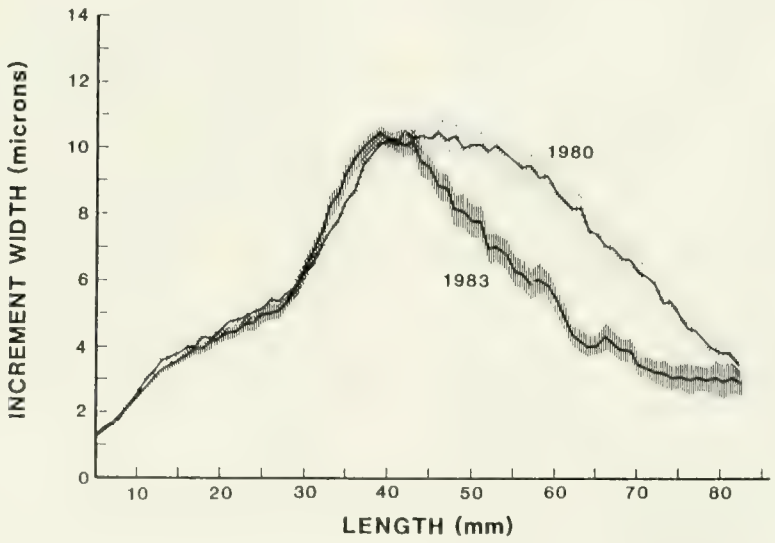

FIGURE 2.—Average otolith increment width versus length of 104 northern anchovy spawned in March 1980 and of 99 anchovy spawned in March 1983. Shaded areas are 95% confidence intervals.

than those of 1983 (Figs. 3, 4). Cohorts did not differ significantly in growth until approximately 40 mm. The age of the end of the late larval (10 mm) period was 20 days in 1980 and 19 days in 1983. A local minimum for growth rates of 1983 fish occurred at about 35 mm and at about 42 mm for growth rates of 1980 fish. This corresponds, approximately, to metamorphosis from late larval stage to juvenile stage. The duration of the late larval period (10–35 mm) was about 70 days in both 1980 and 1983.

After metamorphosis, growth rates increased in 1980 and 1983 until about 40 mm. At about 40 mm, the growth rates of the two cohorts diverged, and the mean back-calculated growth rate of the 1983 cohort was well below the estimated 95% confidence interval of the 1980 cohort. Growth rates declined steadily in 1983 at sizes larger than 40 mm, while growth rates of about 0.4 mm/d were sustained in 1980 until almost 60 mm. After 60 mm, growth declined at about the same rate as the decline in the 1983

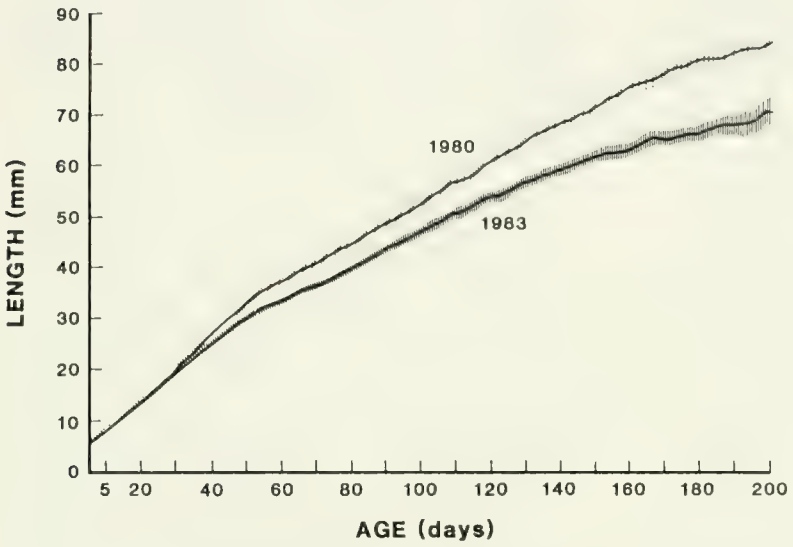

FIGURE 3.—Length versus age of northern anchovy larvae and juveniles of the March 1980 and 1983 cohorts back calculated from daily increments in otoliths.

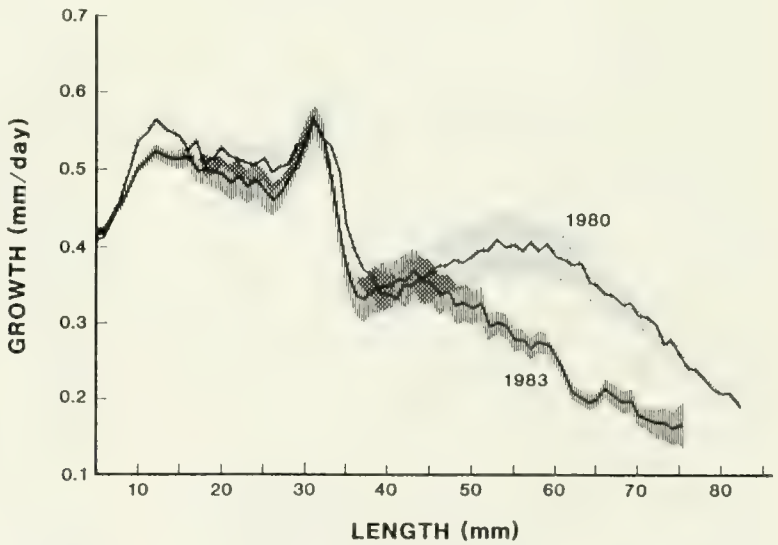

FIGURE 4.—Age-specific growth rates back calculated from daily increment widths of northern anchovy spawned in March 1980 and March 1983. Growth rate of length in mm per day. Shaded areas are 95% confidence intervals.

cohort. Growth within cohorts varied most between 40 and 60 mm.

In 1980 and 1983, northern anchovy growth in weight increased rapidly at small sizes (Fig. 5). Back-calculated growth rates for 1983 reached a local maximum of 6.5 mg/d at about 40 mm and then declined before slowly increasing to 7.5 mg/d at 79 mm. Back-calculated growth rates for 1980 showed a steady increase to about 11.5 mg/d at about 65 mm, which was maintained until about 75 mm, after which growth declined. The growth of northern anchovies hatched in March 1983 peaked at an earlier time (about June) in 1983 and at a smaller size (40 mm), whereas the growth of anchovies hatched in March 1980 peaked near the end of July 1980 and at a larger size at (about 65 mm).

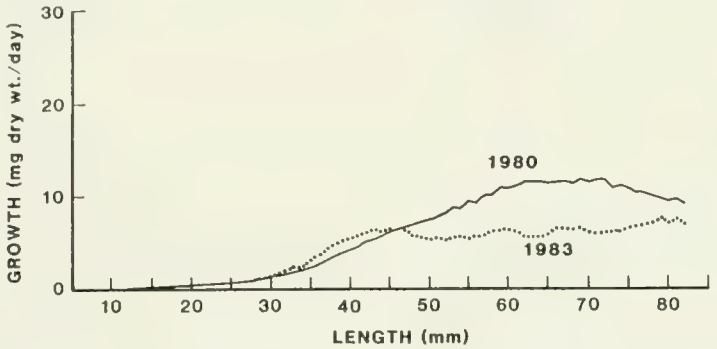

FIGURE 5.—Mean back-calculated growth rates of northern anchovy spawned in March 1980 and March 1983. Growth rate of mass in mg dry weight per day.

DISCUSSION

Growth rates of late larval northern anchovy did not vary in two otherwise extreme years, 1980 and 1983. Methot (1981) found little variance in early larval growth in the sea. Smith (1985) postulated that major changes in recruitment would result from changes in growth rates in the late larval period (10–35 mm) from 0.227 to 0.559 mm/d, a difference of 0.3 mm/d. In this study, however, growth rates of the late larval stage varied by <0.05 mm/d between 1980 and 1983.

Northern anchovy juveniles grew less during 1983 and 1984, compared with the previous three years. Fiedler et al. (1986) also reported reduced growth of anchovy in 1983, but the mean size of 1 yr old fish indicated a dramatic recovery in 1984. This apparent recovery may be in part due to geographic shifts in the population or to changes in spawning date and sampling time in 1984.

When size is adjusted for age and date of spawning, growth of juvenile northern anchovy was reduced in fish hatched in February through April of 1984 compared with fish hatched in the same months in 1980–82 (Fig. 1). This result is consistent with the results from studies of other fish populations on the west coast during El Niño. Growth rates and condition factors were also reduced in the Pacific herring, *Clupea harengus pallasi* (Spratt 1987), the blue rockfish, *Sebastes mystinus* (Van Traskie[2]), and in chinook, *Onchorhynchus tshawytscha*, and coho, *Onchorhynchus kisutch*, salmon (Pearcy and Schoener 1987) during El Niño.

Although the 1982–83 El Nino was fully developed by October 1982 along the coast of Peru, full development of large scale warming off the North American coast did not occur until January 1983 (Lynn 1983). Positive temperature anomalies (>1°C) were evident both at the surface and at depth throughout the California Current (McGowan 1985; Norton et al. 1985). Negative salinity anomalies associated with subsurface temperature anomalies indicated intrusion of low salinity water from the south and west into the Southern California Bight (Simpson 1983).

These temperature anomalies represent a large change in the heat content of the ocean but are small relative to the thermal range of northern anchovy. Thus the small size of juvenile

[2]Van Traskie, D. 1985. Growth of blue rockfish (*Sebastes mystinus*) during El Niño. (Abstr.) Calif. Coop. Fish. Invest. Conf., Idyllwild, CA, Oct. 22–25, 1985.

anchovies during 1983 may be a direct result of reduced food availability at the same time that the rapidly growing juveniles experienced higher metabolic rates due to the elevated environmental temperatures. Zooplankton volumes on CalCOFI line 90 (line 90 intersects the coast at lat 33°29.9′N, long. 117°44.4′W and proceeds seaward on a bearing 240° clockwise from North) were lower than the 95% confidence limit of the 30 year CalCOFI time series (McGowan 1985).

Growth rates were not, however, depressed over the entire early life history. The growth rates of larval stages (5–35 mm) were not significantly different between the two years 1982–83 (Figs. 3, 4). Growth rates in 1983 were reduced in the early juvenile stage, and in particular after 40 mm, compared with growth rates in 1980.

Thus food was not growth limiting until the fish reached a certain size. As fish larvae grow, the ration necessary to sustain growth increases. Since the density of food particles decreases with size (Sheldon and Parsons 1967; Sheldon et al. 1972), at some stage food must become growth limiting. Based on this analysis, food-limited growth is unlikely in anchovies <40 mm during conditions that existed in the Southern California Bight in 1983, and unlikely in anchovies <65 mm during "normal" years such as 1980.

The similarity of back-calculated larval growth rates between years may be a result of the interaction of growth and mortality. A wide range of growth rates are possible at this stage (Hunter 1980), but variable growth rates are not observed in the field. Mortality of slow-growing individuals may reduce the range of growth rates in survivors to metamorphosis.

While the 1957–58 El Niño had a dramatic effect on northern anchovy recruitment in 1958, the numbers of fish in the 1983 and 1984 year classes were not appreciably lower than the previous years (Methot 1988). Thus, although the juvenile period was prolonged in 1983, recruitment was not affected. The major effect of El Niño on the anchovy population was to reduce the size of recruits as well as perhaps the size of adults and the reproductive potential of the 1983 and 1984 cohorts.

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Genetic and Morphometric Variation in the Pacific Sardine, *Sardinops sagax caerulea:* Comparisons and Contrasts with Historical Data and with Variability in the Northern Anchovy, *Engraulis mordax*

Dennis Hedgecock, Elmarie S. Hutchinson, Gang Li,
Frederic L. Sly, and Keith Nelson

ABSTRACT: Pacific sardines from five widely separated localities are found to have little genetic variation both within and between populations. Of the 32 allozyme-coding loci examined from a total of 149 fish, the proportions that are polymorphic within a population (P) range from 7% to 27% with a mean of 12%. Average proportions of heterozygous individuals per locus (H_e) range from 0.5% to 1.6% with a mean of 1.0% over the five populations. Pacific sardine populations are virtually genetically identical at the presumptive gene loci examined. For each locus that is polymorphic in more than one population, the same rare variant allele is shared at about the same frequency, suggesting strongly that there has been gene flow throughout the present range of the species. These results contrast with substantial genetic variation detected within and between northern anchovy populations from the California central stock (average P = 40%, average H_e = 7.5%) and with the significantly higher levels of genetic variation reported for other marine clupeoids. Despite a low level of genetic variation, the Pacific sardine shows a north-south cline in size-at-age that is as steep and as large as that seen in historical, precollapse populations. In the past, such differences were interpreted as evidence of genetically distinct subpopulations. Our results imply that rapid differentiation of growth rate among geographic populations, probably together with differentiation of correlated life history traits, is largely environmentally, and not genetically, determined. It appears that biological data from historical populations can safely be used for area-specific fisheries models of the recovering sardine stocks in California.

A variety of studies have suggested that, prior to its collapse in abundance, the Pacific sardine, *Sardinops sagax caerulea*, comprised two or more distinct subpopulations (morphometry and meristics: Hubbs 1925; Clark 1936, 1947; McHugh 1950; growth: Phillips 1948; Felin 1954; Clark and Marr 1955; Radovich 1962, 1982; movements of tagged fish: Clark and Janssen 1945; Clark and Marr 1955; spatiotemporal distribution of spawning: Ahlstrom 1954, 1959; erythrocyte antigens: Sprague and Vrooman 1962; Vrooman 1964; reviews by Marr 1957; Radovich 1982). Population structure likely played a role in the collapse of the fishery, perhaps directly, by virtue of differences among subpopulations in life history and resilience to fishing pressure (Wisner 1961; Murphy 1966; Radovich 1982) and more certainly, indirectly, by contributing to overestimations of stock size in the waning years of the fishery (MacCall 1979). With the return of substantial numbers of Pacific sardines to the California Current in recent years and the lifting of the fishing moratorium (Wolf et al. 1987) has come interest in management questions such as *which* sardine has recovered and what life history characteristics and yields can be expected (MacCall 1986).

We have made studies of protein and morphological variation in the Pacific sardine to shed light on such questions. Electrophoretic separation of proteins followed by chemical staining to reveal the locations of proteins or specific enzymes allows inferences to be made concerning variation in the genes encoding these proteins. This in turn provides a description, useful for management, of the genetic structures of exploited fish populations (see Ryman and Utter 1987). Several clupeoids, including the northern anchovy, *Engraulis mordax*, which co-occurs with the Pacific sardine in the California Current, have been shown to harbor considerable stores of electrophoretically detectable genetic variability (Hedgecock and Li 1983; Table 8). In this paper, we compare protein and allozyme variation in samples of Pacific sardines collected

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from five widely separated localities with that detected by us in nine trawl samples of northern anchovy taken from the central stock (sensu Vrooman et al. 1981).

MATERIALS AND METHODS

Sardinops sagax

Collections

Samples were collected from Guaymas, Sonora, Mexico (February 1985; Fig. 1, GUAYM; N = 48), Magdalena Bay, Baja California Sur, Mexico (May 1984; MAGDA; N = 37), the Southern California Bight (February–April 1986; Huntington Beach, CA, N = 8; San Pedro, CA, N = 28; pooled into one sample, SOCAL), Monterey Bay, CA (November 1984; MONTE; N = 29) and Tomales Bay, CA (December 1984; TOMAL; N = 5). Whole fish were frozen after collection and transported to the Bodega Marine Laboratory where they were kept at −70°C until thawed for morphometric measurements and dissection of tissue samples for electrophoresis.

Morphological Characters

Measurements of the following 12 morphometric traits were made on partially thawed specimens using either vernier caliper or mounted millimeter rule: a series of lengths measured from the snout to the 1) end of the hypural bones (standard length), 2) anterior margin of the orbit, 3) posterior edge of the maxillary, 4) posterior border of the supraoccipital, 5) posterior edge of the operculum, 6) dorsal-fin origin, and 7) vent, followed by measurements of 8) interorbital width, 9) maximum head width, 10) minimum body depth, 11)

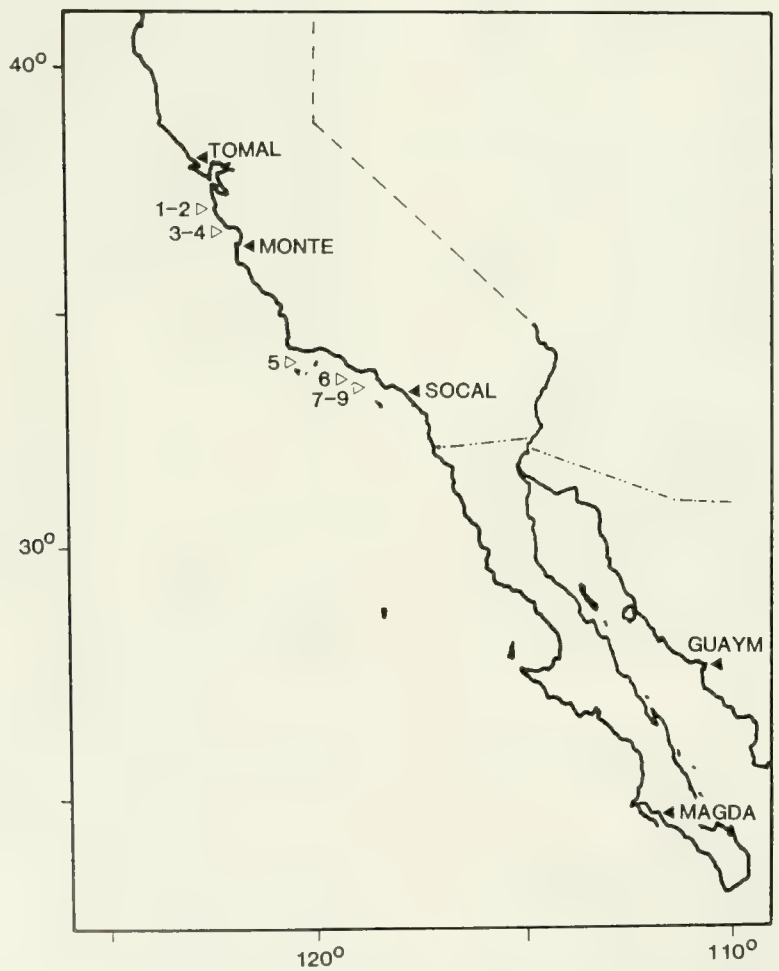

FIGURE 1.—Map showing locations of collections for Pacific sardine (solid arrowheads) and northern anchovy (open arrowheads).

anal-fin-base length, and 12) caudal-peduncle depth.

Tissue Samples

After morphological measurements were made, eye, heart, liver, and skeletal (epaxial) muscle tissues were dissected from each specimen for electrophoretic analyses. Tissue samples were kept in plastic well-trays on ice during dissection, then covered and stored frozen at −70°C for a period of several days prior to electrophoresis. The day before electrophoresis, tissue samples were thawed, equal volumes of 0.5 M Tris-HCl, pH 7.1 buffer were added to the samples, and the tissues were homogenized on ice, by hand, with a ground-glass pestle. Homogenized samples were then returned to the −70°C freezer overnight. On the day of electrophoresis, samples were allowed to thaw slowly on ice.

Otoliths

Sagittal otoliths were removed from specimens and cleared overnight in a 2% KOH solution. They were then rinsed in deionized water for one or more days, air dried, placed by pairs in gelatin capsules with the specimen number, and stored in envelopes labeled by population. Specimen identification for the Magdalena Bay sample was lost.

The age of each specimen was determined by counting otolith annuli following the methods of Collins and Spratt (1969). Each pair of otoliths was placed for examination under water in a separate well (1 cm in diameter and painted black) drilled into a strip of plexiglass. All annuli were counted under a binocular dissection microscope with incident illumination by one of us (F. L. Sly). His recounts agreed with his initial counts (98% consistency); in a comparison test, 80% of his counts were in agreement with those of California State Department of Fish and Game otolith readers.

Electrophoretic Protocol, Genetic Interpretation, and Allozyme Nomenclature

Methods for horizontal starch-gel electrophoresis, protein assays, and genetic interpretation of zymograms were substantially the same as those described previously (Ayala et al. 1973; Tracey et al. 1975; Utter et al. 1987). The protocol used to separate and resolve 20 enzymes or proteins inferred to be encoded by a total of 32 genes is summarized in Table 1. Nomenclatures for proteins, for genes inferred to encode these proteins, and for alleles at these genes are detailed by Utter et al. (1987). Proteins are referred to by the capitalized abbreviations given in Table 1 and the corresponding genes by these same abbreviations italicized in upper and lower case. Numerical suffixes distinguish among isozymes or multiple proteins in order of increasing anodal migration. Alleles are symbolized by italicized numerals obtained by adding or subtracting the number of millimeters separating variants from the most common electromorphs observed for each protein. Alleles encoding common electromorphs are arbitrarily designated *100*. Specimens from several populations were included in every electrophoretic run so that repeated comparisons of relative mobilities of their allozymes were made.

Allozyme Data Analysis

Maximum-likelihood estimates of allelic frequencies and observed proportions of heterozygous genotypes at each locus scored in at least two population samples were computed from numbers of individuals in allelic or genotypic categories and the total numbers of genomes ($2N$) or individuals (N) sampled, respectively. Observed and expected proportions of heterozygous genotypes at each locus were averaged over loci to obtain means (Nei's [1978] unbiased estimates of H_o and H_e, respectively). The proportion of genes for which any electrophoretic variation was detected in a population sample was defined as P; for the population sample sizes used, this criterion of polymorphism is close to the frequently used definition that the most common allele cannot exceed a frequency of 0.99 for a polymorphic locus. Averaging of P and H over population samples was done using angular transformation of these proportional values followed by back-transformation of means and confidence limits. Owing to the nature of the results, no further genetic statistics were calculated.

Morphometric Data Analysis

The BMDP multivariate statistical software package (Dixon 1981) was used to perform discriminant function (P7M) and principal component (P4M) analyses on log-transformed morphometric data. Standard settings were used in the discriminant analysis for tolerance (0.01), F-to-

TABLE 1.—Starch-gel electrophoretic protocols used to reveal allozyme variation.

			Pacific sardine			Northern anchovy		
	Enzyme or protein	E.C. no.	Tissue	Buffer[1]	No. loci	Tissue	Buffer[1]	No. loci
AAT	aspartate aminotransferase	2.6.1.1	—	—	—	E	A	1
ADA	adenosine deaminase	3.5.4.4	L	A	1	L	A	1
ADH	alcohol dehydrogenase	1.1.1.1	E	B	1	—	—	—
ADK	adenylate kinase	2.7.4.3	M	D	2	M	D	1
ALDO	aldolase	4.1.2.13	—	—	—	M	B	1
CK	creatine kinase	2.7.3.2	M	D	1	M	D	1
EST	esterase[2]	3.1.1.–	L	A,B	1	L	A	2
FBP	fructose biphosphatase	3.1.3.11	L	B	1	—	—	—
FUM	fumarate hydratase	4.2.1.2	M	C,D	1	M	D	1
GAPDH	glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12	M	C	2	M+E	C	2
GL	dipeptidase[3]	3.4.13.11	E	B	1	—	—	—
GPDH	glycerol-3-phosphate dehydrogenase	1.1.1.8	M	D	1	M	D	1
GPI	glucose-6-phosphate isomerase	5.3.1.9	L,M	D,B	1	L	B	1
HBDH	3-hydroxybutyrate dehydrogenase	1.1.1.30	E+L	B	2	E+L	B	2
HK	hexokinase	2.7.1.1	—	—	—	M	B	1
IDH	isocitrate dehydrogenase	1.1.1.42	H+L	D	2	H	D	1
LAP	leucine aminopeptidase	3.4.11.1	—	—	—	L	A	1
LDH	lactate dehydrogenase	1.1.1.27	L+M	B	2	L+M	B	2
LGG	tripeptidase[4]	3.4.13.4	E	B	1	E,L	B	1
LT	dipeptidase[5]	3.4.13.11	E	B	1	E+L	B	2
MDH	malate dehydrogenase	1.1.1.37	H	D	2	H	D	2
ME	NADP-dependent malate dehydrogenase[6]	1.1.1.40	M	B	1	—	—	—
6PGDH	6-phosphogluconate dehydrogenase	1.1.1.44	E,M	C	1	E,M	C	1
PGM	phosphoglucomutase	2.7.5.1	M	A	1	M	A	1
PNP	purine nucleoside phosphorylase	2.4.2.1	—	—	—	L	E	1
PP	dipeptidase[7]	3.4.13.9	L	B	1	—	—	—
PROT	general proteins[8]	general	E+M	A	4	E+M	A	9
SOD	superoxide dismutase[9]	1.15.1.1	L	B	1	L	B	1
TPI	triosephosphate isomerase	5.3.1.1	—	—	—	M	D	1
XDH	xanthine dehydrogenase	1.1.1.204	—	—	—	L	B	1
	Totals[10]		20 proteins,		32 loci	24 proteins,		39 loci

[1]Buffers A, B, C, and D as described by Tracey et al. (1975); buffer E is the lithium borate discontinuous buffer system 2 of Selander et al. (1971).
[2]α-naphthyl butyrate and β-naphthyl acetate as substrates.
[3]L-glycyl-leucine as substrate.
[4]L-leucyl-glycyl-glycine as substrate.
[5]A 1:1 mixture of L-leucyl-valine and L-leucyl-tyrosine as substrates.
[6]Known as malic enzyme.
[7]L-phenylalanyl-proline as substrate.
[8]Stained with Coomassie blue.
[9]Usually scored on gels stained for HBDH.
[10]Di- and tripeptidases counted as one enzyme in totals.

enter (4.000), F-to-remove (3.996), and prior probabilities (equal).

Engraulis Mordax

Collections

Samples of 48 anchovies were obtained from each of nine midwater trawl stations (Fig. 1) occupied between the nights of 24 January and 1 February 1982, by CalCOFI cruise 8202 aboard the RV *David Starr Jordan* of NOAA Southwest Fisheries Center, La Jolla. CalCOFI grid coordinates (CalCOFI Atlas No. 1, 1963) for these collections and place names assigned to them for convenience were as follows: 1) Half Moon Bay, 63.3:51.0; 2) Half Moon Bay, 63.3:52.0; 3) Santa Cruz, 66.7:49.0; 4) Santa Cruz, 66.7:50.0; 5) Santa Barbara, 81.3:42.4; 6) Point Dume, 85.0:44.0; 7) Santa Monica Bay, 85.8:34.0; 8) Santa Monica Bay, 85.8:36.0; 9) Santa Monica Bay, 85.8:41.0. Whole fish were frozen individually aboard ship at −70°C and then packaged in plastic bags labeled by locality. Frozen packages were shipped by air to the Bodega Marine

Laboratory where they were kept in a −70°C freezer until dissection.

Data Taken on Specimens

Eye, heart, liver, and skeletal muscle tissue samples were taken from each of the 432 northern anchovy used for this study. For all specimens but those from population sample 8, standard length and sex were recorded and otoliths were taken. Annuli were counted by one of us (F. L. Sly) in a manner similar to that described for the sardine, following the methods of Collins and Spratt (1969).

The electrophoretic protocol used to separate 24 proteins encoded by 39 scorable genes is given in Table 1. These proteins were assayed in tissue samples from an average of nearly 46 specimens (minimum of three) from each of the 9 population samples. Genetic interpretation and allozyme nomenclature were as described above for the sardine analysis with the following additions: 1) Gels for polymorphic enzymes were scored independently by the authors D. Hedgecock and Gang Li, and any discrepancy between the two scores was resolved by reexamination and negotiation; and 2) problems with the resolution of certain allozymes from liver tissue became apparent. A pattern of missing IDH-2, missing EST-5, and blurred LDH-3 and HBDH-2 phenotypes—the last mimicking the 100/105 polymorphism—was subsequently associated with degenerated liver tissues in individual specimens or even entire population samples that were, perhaps, not frozen soon enough after trawling. IDH-2 appeared most sensitive to this and was eliminated from the study, except as an indicator of degenerate liver tissue. To correct for potential bias in *Hbdh-2* data, individual HBDH-2 scores were omitted if (i) any other element of the above composite, degenerate-liver zymogram was observed in that individual *and* (ii) missing elements (i.e., IDH-2 and EST-5) were observed in at least one other specimen from the same population sample (to prevent a missing or failed enzyme assay from causing data rejection). Mean number of individuals assayed for HBDH per population sample was thus reduced to 33 ± 3.

Allozyme Data Analysis

Single-individual genotypes were recoded as paired alphabetical characters and submitted to the BIOSYS-1 program of Swofford and Selander (1981) for calculations of allelic frequencies, average proportions of heterozygous individuals per locus (H_o and H_e as defined above), proportions of polymorphic genes (P, where a locus is considered polymorphic if the frequency of the most common allele does not exceed 0.99), chi-square goodness-of-fit tests to Hardy-Weinberg-Castle (H-W-C) equilibrium genotypic proportions using Levene's (1949) correction for small sample sizes, Wright's (1978) F-statistics, and Nei's (1978) unbiased estimates of average genetic identity (I) and genetic distance (D). Averaging of P and H over population samples was done using angular transformation followed by back-transformation of means and confidence limits. Spearman rank correlations of angular-transformed allelic frequencies with the sines of latitude of collection localities, log-likelihood ratio (G) tests of the independence of allelic frequency and locality, and analyses of allelic frequencies cross-classified by locality, sex, and age (ACCCD; Fienberg 1980) were used to evaluate sources of genetic heterogeneity.

RESULTS

Sardinops sagax caerulea

Genetic Variation

We detected electrophoretic variation in the zymograms of seven proteins, including three di- and tripeptidases, from Pacific sardines, (EST-6, FBP, GPDH, IDH-2, LGG, LT, PP, 6PGDH, SOD; Table 2B). There is, however, remarkably little protein polymorphism and individual heterozygosity at the total 32 loci examined in 149 Pacific sardines (Table 2A). The proportion of polymorphic genes ranges from 7.4% in each of the samples from Tomales and Magdalena Bays to 26.9% in the Guaymas sample, with an average of 12.3% (95% C.L.: 6.4–19.6%). Average heterozygosities range from 0.5% in the Magdalena Bay sample to 1.7% in the Guaymas sample, with a mean over all population samples of 1.0% (95% C.L.: 0.6–1.5%). Estimates of genetic variation are probably best for the Guaymas sample, for two reasons: 1) There were generally larger numbers of individuals sampled per gene, which accounts for the finding of rare heterozygotes at *Idh-2*, *Lgg*, and *Pp*, loci that were not well sampled elsewhere. 2) We sampled two moderately polymorphic loci, *Est-6* and *Fbp*, that were not scored in any other large population sample. There are no significant differences between

TABLE 2.—Allozyme variation in five population samples of Pacific sardine.

	Tomales Bay	Monterey Bay	S. Calif. Bight	Magdalena Bay	Guaymas
A. Summary statistics					
No. of fish (N)	5	29	30	37	48
No. of loci	27	27	23	27	26
P (as percent)	7.4	14.8	8.7	7.4	26.9
H_o (as percent)	1.5	1.0	0.6	0.5	1.7
H_e (as percent)	1.5	1.0	0.6	0.5	1.6
B. Polymorphic enzymes[1]					
	Variants	No. of heterozygotes in samples of size (N)			
EST-6	(103)	0 (5)	—	—	—	3 (48)
FBP	(102)	1 (5)	—	—	—	7 (47)
GPDH	(102)	0 (2)	1 (29)	0 (30)	0 (34)	0 (12)
IDH-2	(93)	0 (5)	0 (22)	1 (29)	0 (23)	1 (48)
LGG	(96)	0 (5)	—	0 (30)	0 (7)	1 (48)
LT	(97)	0 (5)	—	0 (30)	0 (7)	1 (48)
PP	(103)	0 (5)	3 (28)	0 (30)	1 (37)	4 (48)
6PGDH	(103+98)	1 (5)	3 (29)	3 (30)	4 (37)	3+1 (48)
SOD	(93)	0 (5)	1 (29)	0 (30)	0 (37)	0 (48)

[1]Zymogram banding patterns of presumptive heterozygotes at the loci inferred to encode these proteins conform to those expected on the basis of known subunit structures: tetrameric structure for FBP; dimeric structure for GPDH, IDH, LGG, 6PGDH, and SOD; monomeric structure for EST-6, LT and PP (Darnall and Klotz 1975; Harris and Hopkinson 1976; Ruth and Wold 1976; Koehn and Eanes 1978; Utter et al. 1987).

observed and expected average heterozygosities in any of the population samples. For no individual locus is it possible to test H-W-C expected genotypic proportions in a population sample, owing to the low frequencies of variant alleles and the relatively small sample sizes.

In addition to the low genetic variation within each of the samples of Pacific sardines, there is almost no variation among populations in the frequencies of allozymes (Table 2B). Except for 6PGDH, for which a third allozyme was inferred from observation of a single 98/103 heterozygous phenotype in the Guaymas sample, all polymorphic allozymes are represented by just two alleles. For each locus that is polymorphic in more than one population, the same rare variant allele is shared at about the same frequency (Table 2B). Thus, the five, widely separated populations of Pacific sardine sampled in our study are virtually genetically identical at the 32 loci examined.

Ageing from Otolith Annuli

Under the assumption that an annulus represents a yearly growth ring and that fish with one ring are one year old, three age classes, 1's, 2's, and 3's, predominate in all five population samples. There are no statistically significant differences in distribution of ages among the four larger samples $\chi^2_{9df} = 10.7083$, $0.1 < P < 0.5$; data in Table 3). Nor is there a difference between the small Tomales Bay sample and the others (Fisher's exact test on Tomales Bay data versus all other data combined, $P > 0.90$).

TABLE 3.—Distributions of ages in five population samples of Pacific sardine.

Age	Tomales Bay	Monterey Bay	S. Calif. Bight	Magdalena Bay	Guaymas
1	0	9	10	19	21
2	4	14	14	13	22
3	1	3	5	1	3
4	0	0	1	0	0
Sample size:	5	26	30	33	46
Mean:	2.2	1.8	1.8	1.5	1.6

Morphological Variation

In contrast to the similarity of age class compositions among population samples, size distributions among sites are grossly different, with sardines from California being much larger than those from Mexico (Fig. 2). Stepwise discriminant function analysis (DFA) of the 12 log-transformed morphometric variates reveals, after 10 steps, significant differences among the five population samples (approximate F = 22.085 with 32, 499 df, $P << 0.001$). However, discrimination is based primarily on log of standard length which enters the discriminant function first with F = 243.49 ($P << 0.001$; 4, 142 df). A principal component analysis (PCA) of those traits contributing to between-group variance in the DFA produces a single factor, heavily and positively loaded by all traits and accounting for 97% of the variance in data space (minimum factor eigenvalue set to 1.0); such a factor is generally interpreted to represent variance in size (Humphries et al. 1981). The evident geographic cline in size apparently reflects a cline in growth rate; at the extremes, fish of the same age from central California and from the Gulf of California can differ in standard length by nearly 100 mm (see Figure 2).

Two further analyses do indicate minor but significant morphological variation attributable to shape differences among sardines from different geographic areas. First, two factors extracted in a PCA of log-transformed variates standardized by subtraction of the log of standard length show complementary patterns of factor loadings suggestive of different allometries of head size relative to body size among populations (Fig. 3A). The separation of populations along the factor 1 axis (Fig. 3B) is *inversely* related to standard length; i.e, larger California fish are on the left of smaller Mexican fish, owing to the negative allometry of head dimensions relative to standard length. This result is consistent with observations on postlarval Pacific sardines (McHugh 1950) as well as with a general geographical pattern in fish morphology (Jensen 1944; Martin 1949).

Second, comparisons of pairs of population samples for which there is considerable overlap in the sizes of specimens (Southern California

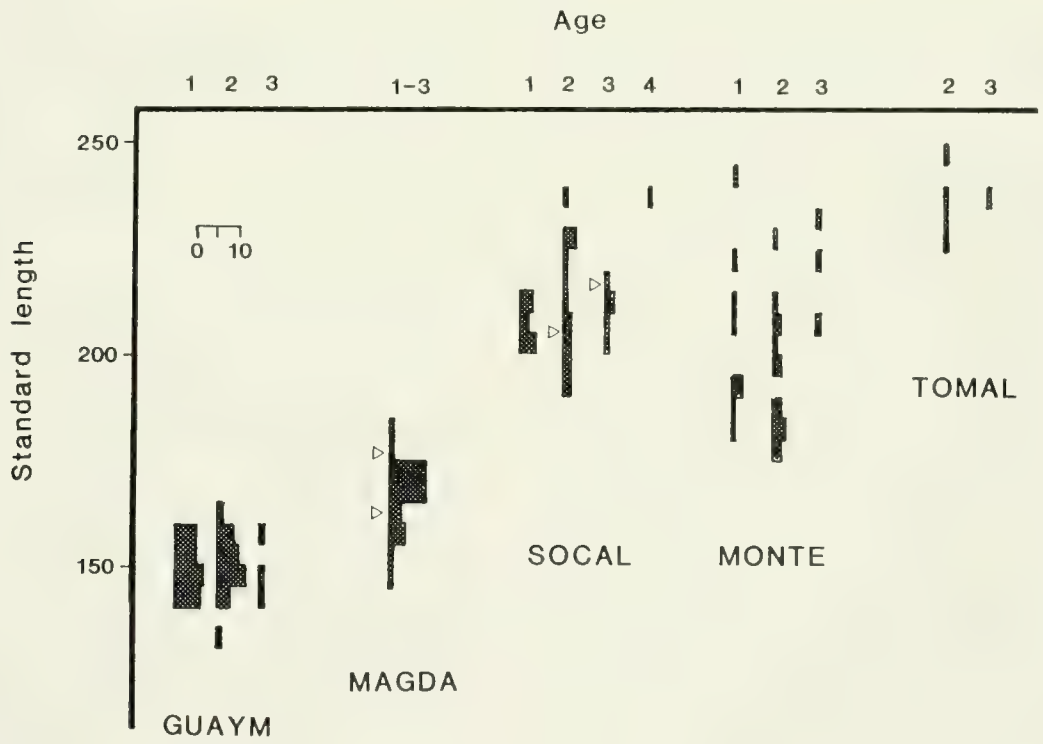

FIGURE 2.—Histograms of standard lengths for various ages of Pacific sardines in five population samples. Open arrowheads along the baselines of the Magdalena Bay and Southern California Bight population samples indicate the mean sizes of two- and three-year-old fish in the 1961–62 sardine catches of Baja California and California, respectively (from Vrooman 1964).

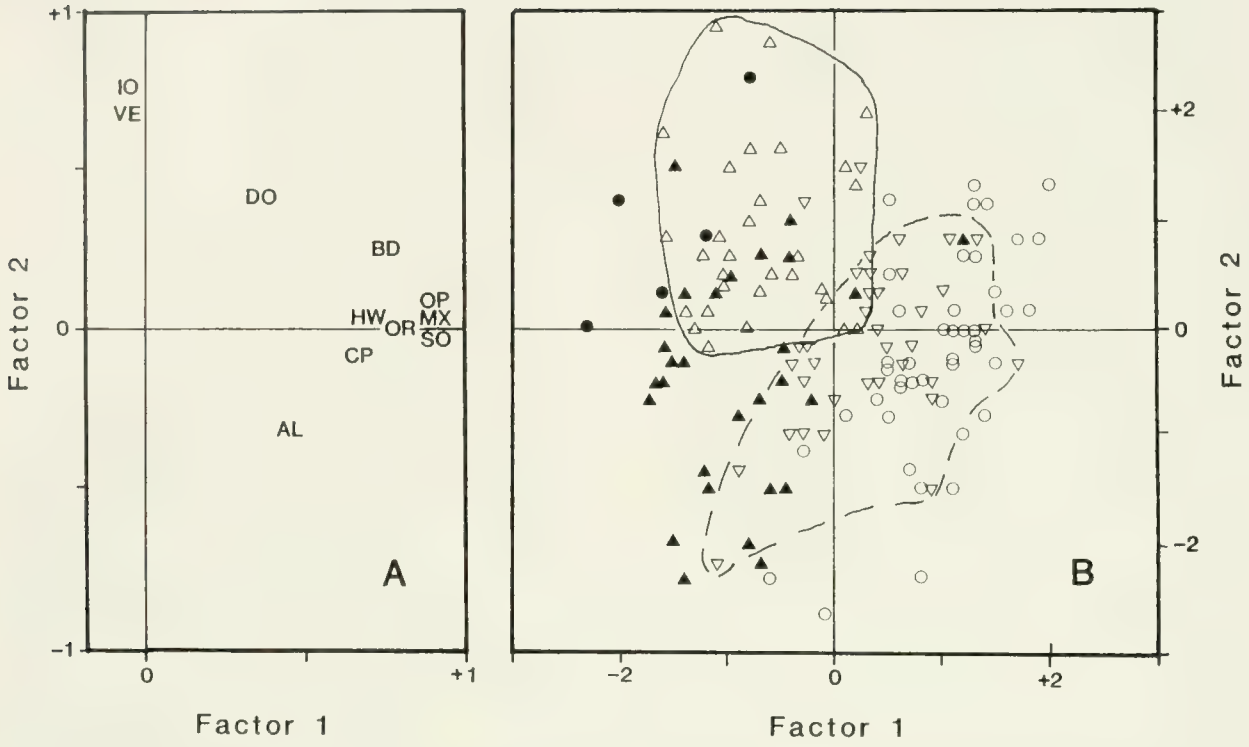

FIGURE 3.—(A) Loadings on the first two factors from a principal components analysis of size-standardized morphometric traits measured on 147 Pacific sardines; I0 = interorbital width, VE = snout to vent length, DO = snout to dorsal-fin origin, AL = anal-fin base length, CP = caudal-peduncle depth, HW = maximum head width, BD = minimum body depth, OR = snout to orbit length, OP = snout to operculum length, MX = snout to maxillary length, SO = snout to supraoccipital length. (B) Scores for individual sardines on these first two factors. Open triangles, solid line: SOCAL; open inverted triangles, dashed line: MAGDA. Other populations are solid circles, TOMAL; solid triangles, MONTE; open circles, GUAYM (see Figure 1).

Bight vs. Monterey Bay and Magdalena Bay vs. Guaymas) also show variation in head : body-size allometry. A standard length range of 192–240 mm defines a subset of the Monterey Bay sample comprising 17 individuals whose mean length is identical to that of the 30 southern California specimens. DFA of log-transformed variates takes two steps to produce significant between-group variance (F = 13.344, $P << 0.001$; 2, 44 df) and an average percent correct assignment in a posteriori classifications of 77% (Table 4A). The two characters used in the classification functions are interorbital width and head width (Table 4A). Between subsets of similarly sized fish (145–162 mm) from Guaymas (N = 37) and Magdalena Bay (N = 11), DFA of nine log-transformed variates (three were discarded to keep the number of variates less than N = 11 for Magdalena Bay) produces significant variance in three steps (F = 17.568, $P << 0.001$; 3, 44 df) and 90% correct classification (Table 4B). Maxillary length, interorbital width, and length of anal-fin base contribute to the classification functions for these two Mexican populations (Table 4B).

Engraulis mordax

Genetic Variation Within Populations

Electrophoretic variation was detected in all northern anchovy proteins examined except ALDO and CK. From this variation in protein phenotypes, we infer that our samples of northern anchovy populations contain substantial levels of individual genetic variation (Table 5). Over the 39 loci examined, the average number of alleles per locus per population is 1.61 ± 0.02, ranging from 1.49 ± 0.13 in the inshore Half Moon Bay sample to 1.72 ± 0.16 in the offshore Santa Cruz sample. Proportions of polymorphic loci per population range from 33.3% in the inshore Half Moon Bay sample to 46.2% in the middle station of the Santa Monica Bay transect; mean P over the nine samples is 39.8% (95% C.L.: 37.2–42.5%). Average expected hetero-

TABLE 4.—Classification functions and a posteriori (jackknifed) classifications from discriminant function analyses of similarly sized Pacific sardines from (A) California and (B) Mexican population samples.

A. California's classification functions:

Variate	Monterey	S. Calif. Bight
log interorbital	−668.284	−597.504
log head width	2437.560	2357.524
constant	−1311.788	−1274.079

Population sample (192–240 mm)	% correct classification	Cases classified in sample		
		Monterey	S. Calif. Bight	*N*
Monterey Bay	82.4	14	3	17
S. Calif. Bight	73.3	8	22	30

B. Mexico's classification functions:

Variate	Guaymas	Magdalena Bay
log maxillary	3061.400	2871.099
log interorbital	−449.694	−537.635
log anal-fin base	521.755	591.291
constant	−2006.101	-1949.291

Population sample (145–162 mm)	% correct classification	Cases classified in sample		
		Guaymas	Magdalena Bay	*N*
Guaymas	89.2	33	4	37
Magdalena Bay	90.9	1	10	11

zygosities range from 6.9% in the inshore Half Moon Bay and Point Dume samples to 8.0% in the middle Santa Monica Bay sample, with a mean over the nine samples of 7.5% (95% C.L.: 7.1–7.9%). There are no significant differences between observed and expected average heterozygosities in any of the samples.

Sample sizes and levels of polymorphism permit goodness-of-fit tests to H-W-C genotypic proportions in 27 cases, involving five loci—*Fum*, *Hbdh-2*, *Lgg*, *Pgm*, and *Xdh*. Prior to 14 of these tests, rare alleles were pooled and the frequencies of composite genotypic classes recalculated accordingly (Pamilo and Varvio-Aho, 1984). The probability assigned to a significant deviation from the H-W-C (null) hypothesis, $P_{\alpha 0.05}$, was adjusted for multiple testing by dividing $\alpha_{0.05}$ by the number of populations over which a given locus was simultaneously tested (Cooper 1968). None of the 27 tests is significant at the adjusted $\alpha_{0.05}$ level, although chi-square values for *Hbdh-2* in the offshore Santa Cruz sample and for *Lgg* in the Point Dume sample come close.

Deviations from H-W-C equilibrium for *Hbdh-2* and *Lgg* tend towards excess heterozygotes. Wright's (1978) fixation indices (F_{IS}) for *Hbdh-2* in population 4 and for *Lgg* in populations 4, 6, and 8 (four chi-square tests with $P \leq 0.06$) are −0.49, −0.37, −0.36, and −0.19, respectively. Averaged over populations and alleles, F_{IS} for *Hbdh-2* and *Lgg* is −0.13 and −0.175, respectively; the weighted average F_{IS} over all loci is −0.045 (see Table 7). There is, owing to these excesses of heterozygotes within population samples, an overall excess of heterozygotes in the total population sampled (mean F_{IT} over all loci and populations is −0.012), despite divergence among populations (next section), which is expected to reduce heterozygosity (Wahlund 1928).

Genetic Variation Between Populations

Eleven loci were polymorphic enough throughout the nine population samples (Table 6) to permit analyses of geographical heterogeneity in allelic frequencies. Rare alleles were pooled into one class for all but the *Lgg* and *Xdh* loci, for which two rare-allele classes were formed. The resulting two- or three-by-nine matrices were tested for r × c independence by log-likelihood

TABLE 5.—Summary statistics for three measures of genetic diversity in northern anchovy.

Population sample (CalCOFI grid no.)[1]	Mean sample size per locus (SE)	Mean no. alleles per locus (SE)	% loci polymorphic	Mean heterozygosity	
				Observed (SE)	Expected (SE)
1. Half Moon Bay (63.3:51.0)	44.1 (1.4)	1.49 (0.13)	33.3	7.6 (2.6)	6.9 (2.3)
2. Half Moon Bay (63.3:52.0)	45.7 (1.0)	1.59 (0.14)	35.9	7.9 (2.6)	7.3 (2.3)
3. Santa Cruz (66.7:49.0)	45.4 (1.1)	1.51 (0.11)	41.0	7.1 (2.3)	7.6 (2.4)
4. Santa Cruz (66.7:50.0)	46.3 (0.8)	1.72 (0.16)	41.0	8.70 (2.4)	8.0 (2.5)
5. Santa Barbara (81.3:42.4)	45.9 (1.3)	1.64 (0.17)	35.9	7.9 (2.5)	7.3 (2.3)
6. Point Dume (85.0:44.0)	46.6 (1.1)	1.59 (0.14)	41.0	6.9 (2.5)	6.9 (2.3)
7. Santa Monica Bay (85.8:34.0)	46.3 (0.8)	1.64 (0.14)	43.6	8.1 (2.6)	7.8 (2.4)
8. Santa Monica Bay (85.8:36.0)	42.6 (1.7)	1.67 (0.13)	46.2	8.7 (2.5)	8.8 (2.4)
9. Santa Monica Bay (85.8:41.0)	46.8 (0.4)	1.62 (0.14)	41.0	6.9 (2.2)	7.3 (2.3)
Averages: (SE or 95% C.L.)	45.5 (0.5)	1.61 (0.02)	39.8 (37.2-42.5)	7.8 (7.3-8.2)	7.5 (7.1-7.9)

[1]California Cooperative Oceanic Fisheries Investigations (1963).

TABLE 6.—Frequencies of allozymes for 11 polymorphic enzymes[1] in northern anchovy samples.

Locus (*N*) Alleles	Population samples								
	1	2	3	4	5	6	7	8	9
Est-5									
(*N*)	44	48	37	47	44	48	41	22	40
98	0.011	0.0	0.0	0.011	0.011	0.01	0.061	0.0	0.013
100	0.966	0.948	0.973	0.957	0.955	0.948	0.915	0.909	0.925
101	0.0	0.0	0.0	0.011	0.0	0.021	0.012	0.0	0.025
102	0.023	0.042	0.027	0.021	0.023	0.021	0.012	0.091	0.038
103	0.0	0.01	0.0	0.0	0.011	0.0	0.0	0.0	0.0
Fum									
(N)	48	48	48	48	48	48	48	47	48
96	0.021	0.0	0.01	0.01	0.0	0.0	0.01	0.0	0.0
100	0.5	0.615	0.479	0.573	0.458	0.51	0.573	0.585	0.49
104	0.479	0.385	0.51	0.417	0.542	0.49	0.417	0.415	0.51
Gpi									
(*N*)	48	48	48	48	48	48	48	47	48
90n	0.0	0.0	0.0	0.0	0.0	0.01	0.01	0.0	0.0
96	0.0	0.0	0.0	0.01	0.021	0.01	0.01	0.0	0.01
100	0.979	0.969	0.958	0.958	0.958	0.969	0.958	0.798	0.927
103	0.021	0.021	0.042	0.01	0.01	0.01	0.0	0.202	0.042
105	0.0	0.01	0.0	0.021	0.01	0.0	0.021	0.0	0.021

TABLE 6.—*Continued.*

Locus (*N*) Alleles	Population samples 1	2	3	4	5	6	7	8	9
Hbdh-1									
(*N*)	48	48	48	48	48	48	48	48	48
90	0.0	0.01	0.0	0.0	0.0	0.0	0.0	0.0	0.0
92	0.01	0.0	0.0	0.0	0.01	0.0	0.0	0.0	0.0
96	0.042	0.0	0.0	0.021	0.042	0.042	0.0	0.0	0.02
98	0.01	0.031	0.021	0.021	0.01	0.0	0.031	0.021	0.0
100	0.938	0.948	0.979	0.958	0.927	0.958	0.969	0.979	0.979
103	0.0	0.01	0.0	0.0	0.01	0.0	0.0	0.0	0.0
Hbdh-2									
(*N*)	28	29	32	32	41	48	31	17	40
100	0.821	0.741	0.547	0.516	0.732	0.927	0.597	0.765	0.837
105	0.179	0.259	0.453	0.484	0.268	0.073	0.403	0.235	0.162
Ldh-1									
(*N*)	48	48	48	48	48	48	48	48	48
96	0.115	0.208	0.188	0.125	0.198	0.198	0.125	0.146	0.135
100	0.885	0.792	0.813	0.875	0.802	0.802	0.875	0.854	0.865
Lt-1									
(*N*)	48	48	48	48	48	48	48	48	48
96	0.0	0.021	0.0	0.021	0.01	0.0	0.0	0.021	0.01
100	0.948	0.958	0.948	0.938	0.948	0.99	0.969	0.885	0.938
103	0.052	0.021	0.052	0.042	0.042	0.01	0.031	0.094	0.052
Lgg									
(*N*)	48	48	48	48	48	48	48	48	48
97	0.021	0.021	0.083	0.01	0.042	0.021	0.031	0.052	0.0
100	0.646	0.66	0.74	0.604	0.708	0.583	0.563	0.583	0.688
104	0.333	0.319	0.177	0.385	0.25	0.385	0.365	0.365	0.313
107	0.0	0.0	0.0	0.0	0.0	0.01	0.042	0.0	0.0
6Pgdh									
(*N*)	48	48	48	48	48	48	48	48	48
98	0.021	0.01	0.021	0.052	0.0	0.0	0.0	0.01	0.021
100	0.979	0.979	0.969	0.948	0.99	1.0	0.969	0.958	0.979
104	0.0	0.01	0.01	0.0	0.01	0.0	0.031	0.031	0.0
Pgm									
(*N*)	48	48	48	47	48	48	48	48	48
96	0.0	0.01	0.0	0.01	0.0	0.01	0.0	0.0	0.0
98	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.01	0.0
100	0.708	0.677	0.74	0.667	0.771	0.76	0.813	0.833	0.844
103	0.292	0.313	0.26	0.323	0.229	0.229	0.188	0.156	0.156
Xdh									
(*N*)	48	48	48	48	48	48	48	39	48
98	0.177	0.125	0.031	0.167	0.156	0.281	0.135	0.0	0.365
100	0.792	0.844	0.854	0.823	0.823	0.719	0.792	0.744	0.604
102	0.031	0.031	0.115	0.01	0.021	0.0	0.073	0.256	0.031

[1]Zymogram banding patterns of presumptive heterozygotes conform to those expected on the basis of known subunit structures: tetrameric structure for FUM and LDH-1; dimeric structure for GPI, HBDH-1, HBDH-2, LGG, and 6PGDH; monomeric structure for EST-5, LT-1 and PGM; XDH not separated well enough to confirm tetrameric structure (see Table 2 for references).

ratios (G, Table 7). For five of the 11 loci, allelic frequencies are significantly nonindependent of locality; significant heterogeneity of allelic frequencies corresponds to F_{ST} values ≥ 0.019. Considering just the 11 polymorphic loci, Nei's (1978) unbiased genetic identity and distance statistics for 36 pairs of population samples average 0.992 ± 0.001 and 0.008 ± 0.001, respectively; over all 39 loci these statistics average 0.998 ± 0.0003 and 0.002 ± 0.0003, respectively.

Further analyses show that some of the heterogeneity in allelic frequencies is geographically patterned, some is associated with genetic differences between the sexes and among age classes, but that most is not associated with any obvious environmental or biological factor. Allelic frequencies at two of the five variable loci, *Pgm* and *Xdh*, are significantly correlated with latitude (Fig. 4). An attempt was made to examine the dependence of gene frequencies on sex and age as well as locality, but analyses of cross-classified data are made difficult by small sample sizes and uneven distributions of sexes and age classes over localities. In tests of three-factor (LOCALITY × SEX × ALLELIC FREQUENCY) log-linear models for *Hbdh-2*, *Lgg*, *Pgm* and *Xdh*, sex was found to be associated with ALLELIC FREQUENCY only for *Hbdh-2*, for which a fully saturated model with all three pairwise interactions among factors appeared to be the best fit. In 15 tests of log-linear models of AGE × SEX × ALLELIC FREQUENCY within individual population samples, only four could *not* be fit by the model of complete factor independence (*Hbdh-2* in population 9, *Lgg* in population 4, *Pgm* in populations 3 and 4). AGE and ALLELIC FREQUENCY were associated only for *Pgm* in the inshore Santa Cruz sample, for which, again, a fully saturated model was the best fit. Interestingly, interactions of AGE and SEX independent of (or only conditionally associated with) ALLELIC FREQUENCY were significant in all four cases; an association of older males with younger females appeared to be responsible for this.

TABLE 7.—F-statistics and log-likelihood ratio (G) tests of allelic frequency x locality independence for polymorphic loci in nine population samples of northern anchovy.

Locus	F_{IS}	F_{IT}	F_{ST}	G	df	Sig.[1]
Est-5	0.083	0.095	0.012	5.53	8	ns
Fum	0.006	0.019	0.013	11.21	8	ns
Gpi	0.069	0.123	0.057	31.14	8	***
Hbdh-1	−0.040	−0.027	0.012	8.05	8	ns
Hbdh-2	−0.130	−0.037	0.082	57.66	8	***
Ldh-A	0.043	0.051	0.008	7.28	8	ns
Lt-1	0.033	0.046	0.013	13.06	8	ns
Lgg	−0.175	−0.153	0.019	37.98	16	**
6Pgdh	−0.036	−0.021	0.015	11.19	8	ns
Pgm	−0.067	−0.047	0.019	16.68	8	*
Xdh	0.006	0.067	0.062	130.15	16	***
Means:	−0.045	−0.012	0.032			

[1]Probability levels for significance of G-tests are * = $0.01 < P < 0.05$; ** = $0.001 < P < 0.01$; *** = $P < 0.001$.

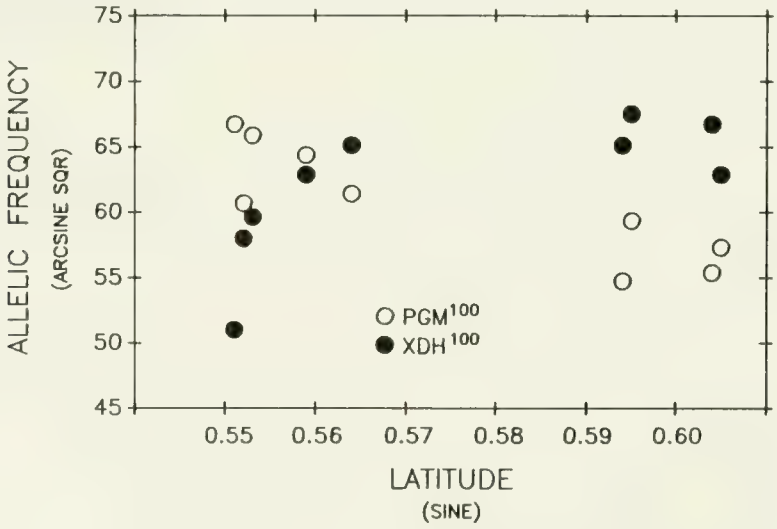

FIGURE 4.—Frequencies of the common alleles for *Pgm* and *Xdh* (arcsine-square-root transformed) plotted against the sine of latitude of collection site. Spearman rank correlation coefficients for the two loci are $r_S = -0.783$, $t = -3.330$ for *Pgm* and $r_S = 0.812$, $t = 3.681$ for *Xdh*.

DISCUSSION

Low Genetic Variation in the Pacific Sardine

Relative to other clupeoids, the Pacific sardine, *Sardinops sagax*, is depauperate in allozyme variation. Direct comparison with the northern anchovy, *Engraulis mordax*, in this study shows that the Pacific sardine has less than 25% of the average heterozygosity of the northern anchovy (Table 2A vs. Table 5). The northern anchovy, not the Pacific sardine, appears to have levels of variation typical of those reported in allozyme studies of clupeoids (Table 8). Average heterozygosity for 15 marine species of the order Clupeiformes is 7.1% (95% C.L.: 6.0–8.2%). The average expected heterozygosity for the Pacific sardine, 1.0%, and even the slightly greater heterozygosity found in the Guaymas population sample, 1.6% fall significantly below the clupeoid distribution ($z = -4.02$, $P < 0.000033$ and $z = -3.39$, $P < 0.0003$, respectively).

There is so little variation within and between Pacific sardine populations that it is not possible to test whether distributions of genotypes conform to the expectations of random mating or whether allelic frequencies are heterogeneous throughout the range of populations sampled. That sardines in widely separated localities have the same rare alleles (Table 2B) suggests strongly, however, that there has been substantial gene flow among contemporary populations (Slatkin 1985).

TABLE 8.—Allozyme variation reported for marine species of the order Clupeiformes.

Species	No. of pops studied	No. of loci studied	Mean no. alleles per locus	Percent loci polymorphic[1]	% mean heterozygosity Obs.	% mean heterozygosity Exp[2]	References[3]
Clupeidae							
Clupeinae							
Opisthonema							
bulleri	2	29	1.4	20.7	5.4	5.5	(1)
medirastre	2	29	1.3	27.6	8.5	7.7	(1)
libertate	5	29	1.6	31.0	6.3	6.7	(1)
Sardinops							
sagax	5	27	1.4	14.5	1.0	1.0	this study
melanosticta	1	22	—	22.7	6.4	—	(2)
Clupea							
harengus	6	40	—	47.5	—	6.5	(3)
harengus	3	25	1.8	38.8	—	7.0	(4)
harengus	14	42	—	21.3	4.8	—	(5)
pallasi	21	40	—	65.0	—	8.3	(6)
pallasi	1	17	—	29.4	5.8	—	(2)
Sprattus							
antipodum	2	13	1.7	50.0	9.6	11.2	(7)
sp.	1	13	1.6	46.2	5.5	5.7	(7)
Dussumieriinae							
Spratelloides							
gracilis	2	16	1.5	24.7	4.0	—	(8)
sp.	2	14	1.5	32.1	4.6	—	(8)
Engraulidae							
Engraulinae							
Engraulis							
japonicus	1	22	—	36.4	6.7	—	(2)
capensis	31	31	—	48.3	—	11.5	(9)
mordax	9	39	1.6	39.8	7.7	7.5	this study
Stolephorus							
heterolobus	3	18	1.7	22.2	10.1	—	(8)
devisi	3	19	1.7	17.1	6.8	—	(8)

[1]Polymorphism defined either as $P_{0.99}$ or inclusive of all observed variation.
[2]H_e are either unbiased estimtes (Nei 1978) or simple averages.
[3](1) Hedgecock et al. 1988; (2) Fujio and Kato 1979; (3) Grant 1984; (4) Andersson et al. 1981; (5) Kornfield et al. 1982; (6) Grant and Utter 1984; (7) Smith and Robertson 1981; (8) Daly and Richardson 1980; (9) Grant 1985a.

By contrast, the substantial allozyme polymorphism in the northern anchovy allows tests of both random mating and spatial homogeneity of allelic frequencies. Chi-square goodness-of-fit tests detect no significant departures from the genotypic proportions expected under random mating, although substantial excesses of heterozygotes are found at the *Hbdh-2* and *Lgg* loci. While liver-tissue degradation may have contributed to this result for *Hbdh-2* (see Materials and Methods), this explanation cannot hold for *Lgg*, which was scored reliably from both liver and eye zymograms. Differences in allelic frequencies either among age classes or between sexes can produce excess heterozygosity, and significant interaction of sex and allelic frequency is detected by fitting of log-linear models to *Hbdh-2* data. For *Lgg*, on the other hand, sex and allelic frequency are independent given locality. It must be remembered that the chi-square test of Hardy-Weinberg-Castle equilibrium has little power to detect failure of its basic assumptions, notably no selection at the locus and an infinite, unsubdivided population (Wallace 1958; Lewontin and Cockerham 1959).

The northern anchovy, again in contrast to the Pacific sardine, appears to have a complex population structure as evidenced by significant heterogeneity of allelic frequencies at 5 of 11 polymorphic loci (Table 7), correlations of some alleles with latitude (Fig. 4), and dependence of some allelic frequencies on sex and age. This heterogeneity is unexpected. All samples were collected within the area occupied by the central stock, which has been considered a single, randomly mating population, primarily on the basis of transferrin-allele frequencies and meristic data (Vrooman et al. 1981; see MacCall et al. 1983). Differences among populations within this area have nevertheless been described for growth and age composition (Parrish et al. 1985), size-adjusted otolith weight (Spratt 1972), size at age (Collins 1969; Mais 1974; Mallicoate and Parrish 1981), seasonality of spawning (Mais 1974; Parrish[1]), and migration patterns (Haugen et al. 1969; Mais 1974), together with between-year variation in many of these life history traits. Similar genetic heterogeneity of anchovy stocks has been described for *Engraulis encrasicholis* (Altukhov et al. 1969a, b; Dobrovolov 1978), although homogeneity of allelic frequencies was reported by Grant (1985b) for *E. capensis*.

For loci polymorphic over the nine population samples, Wright's (1978) measure of average genetic variance among populations, F_{ST}, and Nei's (1978) average genetic distance D—two measures that are maximized by allele replacement among populations—are both relatively small: 0.032 and 0.008, respectively. Significant heterogeneity of allelic frequencies without substantial allele replacement may reflect population subdivision and differentiation resulting from ecological, rather than historical processes. We will explore the causes of this paradoxical genetic heterogeneity in subsequent reports drawing on much larger sets of allozyme, sex, age, and morphological data for northern anchovy collected between 1982 and 1985.

Why does the Pacific sardine have low genetic variation? One possibility is that this species originally had levels of variation typical of clupeoids, but that much of this was lost in the collapse of the California sardine fishery in the 1950's and early 1960's. That this fishery collapse did *not* constitute a population genetic bottleneck, however, appears likely for several reasons. First, the genetically effective population size during the bottleneck would have had to have been very small, on the order of 10 or fewer individuals, in order to account for the current low level of heterozygosity (Chakraborty and Nei 1977). Second, sardine populations in southern Baja California and in the Gulf of California were unaffected by the collapse of the California fishery (Murphy 1969; Sokolov 1974), yet these populations today show low variation also. Finally, by analogy, the Japanese sardine, *Sardinops melanosticta*, which also experienced a severe fishery collapse in the 1940's but has since recovered (Kondo 1980), does not have reduced levels of genetic variation (Fujio and Kato 1979; Table 8).

Alternatively, a restriction in population size in the more distant past might explain low variation in the Pacific sardine. The historical record of scale deposits in varved, anaerobic marine sediments of the Santa Barbara Basin, southern California, does show that, relative to northern anchovy and Pacific hake, Pacific sardines were always less abundant and much more frequently absent (Soutar 1967; Soutar and Isaacs 1969, 1974). Over the past 1,850 years, the Pacific sardine was abundant during 12 periods, each lasting from 20 to 150 years. Intervals between these periods of abundance

[1]Parrish, R. H. 1983. Evidence for a fall spawning anchovy stock. Paper presented at 1983 CalCOFI Conference.

lasted, on average, 80 years and ranged in duration from 20 to 200 years (Soutar and Isaacs 1969). One or more of these periods of low abundance could have been a severe enough bottleneck to cause loss of variation, but this hypothesis may be difficult to falsify. According to Fitch (1969), fossil remains of *Sardinops* are absent from samples of California Pliocene and Pleistocene sediments, whereas evidence of five other pelagic species (*Clupea pallasi*, *Engraulis mordax*, *Merluccius productus*, *Scomber japonicus*, and *Trachurus symmetricus*) is present in at least some samples. This raises the possibility that *Sardinops sagax caerulea* may be a recent arrival in the California Current System and that the low variation is attributable to a small number of founders rather than to a subsequent bottleneck.

Other than such historical hypotheses, we can pose no ecological explanation of low genetic variation (such as provided for decapod crustaceans by Nelson and Hedgecock 1980, for example); the ecology of the Pacific sardine does not appear to be unique relative to those clupeoids having higher levels of variation (Blaxter and Hunter 1982). So we are left at present with no compelling hypothesis to explain the observation of low genetic variation in the Pacific sardine.

Structures of Historical and Contemporary Populations of the Pacific Sardine

Sprague and Vrooman (1962) and Vrooman (1964) described three genetically distinct subpopulations of *Sardinops sagax caerulea* on the basis of significantly different frequencies of a C-positive blood factor (13.6% in samples taken from California waters, 6.0% in samples taken from Baja California, and 16.8% in fish from the Gulf of California). Regrettably, though understandably, electrophoretic separation of allozymes has completely supplanted immunological methods for studying population structure. Data comparable in quantity and quality to historical data on serotype frequencies would be difficult to gather today. A considerable drawback to the immunological method is the requirement for fresh blood, whereas allozymes can be readily obtained from fresh or fresh frozen, muscle or visceral tissues. Moreover, allozyme methods allow a much larger survey of genes than does blood typing; this, in turn, provides for statistical analyses of genetic diversity that take into account the large component of variance among loci (Nei 1978).

Our finding of low genetic variation across a widespread sampling of Pacific sardines contradicts the hypothesis that there are currently genetically different, geographic subpopulations of Pacific sardine. Combined with the recency of the Pacific sardine's reexpansion into the California Current (Wolf et al. 1987), our observations support the alternative hypothesis that this species comprises a single, homogeneous gene pool. Examination of the distributions and abundances of sardine eggs and larvae (Ahlstrom 1954, 1957) does suggest the possibility of dispersal around the tip of Baja California, particularly during cold-water (anti-El Niño) years.[2] Our data on the sharing of rare alleles by widely separated populations support this conjecture by implying a high rate of gene flow throughout the range of the species (Slatkin 1985).

The present study does not falsify the subpopulation hypothesis for historical sardine populations, but our data show that it is unlikely. The former hypothesis requires that only a single southern subpopulation survived the fishery collapse to repopulate the Gulf of California, the Pacific coast of Baja California Sur, and more recently, the California Current. Data on the frequency of C-positive blood type in contemporary sardine populations would be useful. However, morphological and life history data also played an important role in past inferences concerning the structure of historical sardine populations (Radovich 1982). The implications of our data on morphological variation among contemporary populations are discussed next.

Morphological and Life History Variation Among Historical and Contemporary Pacific Sardine Populations

Life history traits, such as the schedules of age-specific growth, mortality, and reproduction, and the covariances among these traits, determine responses by fish populations to exploitation (Cushing 1973; Nelson and Soulé 1987). Indeed, the historical biology of the California sardine fishery and its demise provides an elegant example of this axiom. An important

[2]R. A. Schwartzlose, Centro de Investigaciones Biologicas de Baja California sur and Scripps Institution of Oceanography, La Jolla, CA 92093, pers. commun. 1988.

feature of the collapse of the sardine fishery was its north-to-south progression, which owed greatly to the interaction of underlying life history variation (in particular, steep north-south clines in size-at-age, age of first reproduction, maximum size, and the schedule of natural mortality), geographical shifts in fishing pressure, and natural between-year variation in recruitment (Murphy 1966; Radovich 1982). That life history variation was built upon genetic differences among geographic populations, however, now appears unlikely from the results of our study.

The single, most obvious component of morphological variation in Pacific sardines today is a geographic cline in size-at-age that is as steep and as large as that seen in historical populations (Fig. 2). In the past, such differences were used by several authors to infer the existence of genetically distinct subpopulations, yet the differences have been reestablished in genetically homogeneous, contemporary populations within just a few generations. This implies that rapid differentiation of growth rate among geographic populations—probably together with differentiation of correlated life history features such as age at first reproduction, maximum size, and age-specific mortality (Clark and Marr 1955; Blaxter and Hunter 1982)—is largely environmentally, and not genetically, determined. This is not to say that there are not genes that determine life history traits; but variation of these genes cannot be responsible for geographic variation in life history. The genotype of the Pacific sardine must instead provide for remarkable plasticity in life history phenotype.

One must now be skeptical of the interpretation that life history differences among historical sardine populations were conditioned by genetic differences among subpopulations or races. The question of which sardine stock is now recovering is moot. More importantly, it appears that information on the biology of sardine populations prior to the collapse of the fishery can safely be used for area-specific fisheries models of the recovering stocks.

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Spawning and Survival Patterns of Larval Northern Anchovy, *Engraulis mordax*, in Contrasting Environments—A Site-Intensive Study

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ABSTRACT: During the 1985 spawning season of the northern anchovy, *Engraulis mordax* Girard, off southern California, a serial field study at contrasting sites linked measurable environmental characteristics with parameters of larval anchovy growth and survival and determined a range of environmental conditions over which northern anchovy had recently spawned. Surface and water column characteristics were measured while following surface drifters at each site, and their relation to corresponding measurements of larval anchovy production, growth, mortality, and starvation are reported.

The nearshore site was eutrophic with low current speeds, low wind speeds, and high forage levels which are characteristic of coastal spawning areas. The offshore site, by contrast, was relatively oligotrophic and had higher surface mixing rates, a deeper mixed layer, reduced stability in the pycnocline, and lower forage levels.

Among the measured characteristics of the ichthyoplankton, only one, the larval production rate, was markedly different at the two sites. Although habitat suitability for adult anchovies was different, survival probability for larval anchovies was more equivalent at the two sites than inspection of single parameters of the environment suggested. In contrast with the view that the northern anchovy spawns indiscriminately, the results of this study suggest that components of the adult northern anchovy population tend to spawn under conditions and at levels that yield consistent survival probabilities for their offspring.

Since Lasker's (1975, 1978, 1981) pioneering work on causes of larval fish mortality, recent developments have made techniques available to assess age-specific larval growth, mortality, and physiological condition. These developments have piqued interest in field studies that link environmental processes to survival probabilities for larvae of broadcast spawners. Here we present the results of a site-intensive shipboard study that combined newly available measures of larval condition with a suite of physical and biotic measures of their environment in the Lagrangian setting provided by near-surface drifters to determine local variations of a few days duration. Our results are intended to guide the design and execution of programs that address the recruitment process and its relation to the spawning environment.

Conditions under which northern anchovy, *Engraulis mordax* Girard, spawn and under which their eggs and larvae survive presently are known mainly from cruises of the CalCOFI program, which are quasi-synoptic surveys of broad areas of the spawning domain during which limited sets of environmental observations and measurements have been made (cf. Reid 1988). Owing to limits imposed by time and resources, such surveys do not yield knowledge of the local fate of spawned products because the methods that characterize survival likelihood of larval fish have only recently been developed and verified, and because local changes (those embedded in the surface flow) are not knowable by the survey approach.

METHODS

Site Selection

Criteria for selection of the two study sites were that each must 1) show evidence of recent spawning by anchovy, 2) contrast with the other site in macroscopic setting and environmental character, and 3) exhibit no local gradients indicative of smaller scale (0.1–10 km) environmental

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heterogeneity. The study followed a routine survey by the California Cooperative Fisheries Investigations (CalCOFI Cruise 8502) of the northern anchovy spawning domain. Visual inspection of plankton catches made on this survey yielded estimates of northern anchovy egg abundance at 4–10 nmi intervals. Within areas of high egg abundance, the ship's survey records of 3 m temperature and in vivo phytoplankton pigment fluorescence were scanned for evidence of local gradients. Low variations of pigments and temperature in the vicinity of possible sites were verified by inspection of available satellite images of sea surface temperature and surface layer color, and several sites were then targeted for this study.

At sea, we verified that our criteria held at each site by inspection of plankton tows to confirm recent (and therefore sustained) spawning activity, and by inspection of underway records for local homogeneity of temperature and pigment fluorescence at 3 m depth. We occupied sites shown in Figure 1.

Procedures on Site

Upon verification that a site met the three criteria, we launched a radio-transmitting surface drifter. The ship then moved several nmi to launch a second drifter. Thereafter, we alternated our station pattern between the two drifters, locating each drifter by radio direction-finding equipment and visually. Each site was thus defined, in the Lagrangian sense, to be the water corpus that was moving along with the two drifters. We assumed that both drifters at each site were implanted in macroscopically homogeneous water with respect to physical and biological character. We examine the limits of this assumption by contrasting variations within and between drifters at the same site.

Stations were patterned around each drifter, in turn, at cardinal points 2 km from the drifter. Vertical plankton tows, "CalVETs" (Smith et al. 1985), were made with 150 μm mesh nets from 50 m depth at all four stations to catch fish eggs and larvae to determine age-specific anchovy production and mortality. Oblique bongo tows were made to and from 50 m depth with 333 μm mesh nets and, after we lost the 333 μm mesh nets, with 505 μm mesh nets to catch northern anchovy larvae for estimation of starvation incidence and recent growth rate. At two of the four stations, paired vertical tows similar to CalVETs were made from 50 m depth with 75 μm mesh and 333 μm mesh nets to estimate composition and quantity of larval food rations and of other small plankton, respectively. CTD/Niskin casts were made to 100 m depth at one station, per drifter visit, to measure physical structure of the water column and to get water samples at 10 depths to determine concentrations of particulates, chlorophyll-a and phaeopigments. Secchi depth was determined at one station (daylight permitting) at each drifter to estimate thickness of the euphotic layer. Standard weather observations were made once per drifter visit.

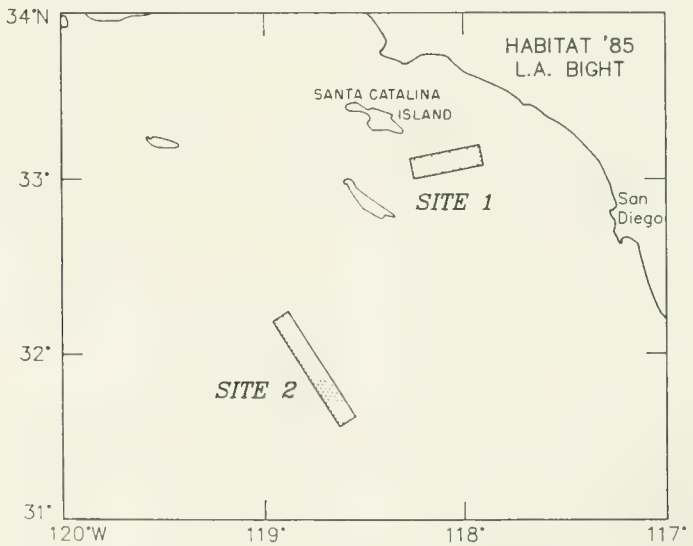


FIGURE 1.—Study site locations in the Southern California Bight.

Environmental Characteristics

Surface Drift

Drifter positions were determined by a combination of satellite navigation, Loran-C, and Decca radar over the course of the study, and were precise within 0.1 km. The drifters were designed as described by Davis et al. (1982) to minimize the effects of wave motion and of wind drag on exposed surfaces, both of which cause deviations of drifter motion from that of water parcels. The 2 km station spacing around each drifter was large compared with precision of drifter position and with deviation of the drifter's motion from surrounding water motion.

Vertical Temperature and Salinity Profiles

Temperature, conductivity, and pressure were recorded with a Neil Brown CTD, following methods used by NOAA/Southwest Fisheries Center.[1] Briefly, 0.25 s scans of temperature, conductivity, and pressure were recorded as the CTD profiled at 20–40 m/min. Conductivity and temperature records corrected for temperature lags are smoothed by a 5–point weighted running mean with binomial coefficients of 1, 4, 6, 4, 1. Salinity was computed using the Practical Salinity Scale of 1978. Salinities and temperature were compared and justified with salinity and temperature values from a hydrographic bottle tripped in the near-surface layer during each cast. Final data were enumerated at 2 m depth intervals.

Phytoplankton Pigments

Chlorophyll-a and phaeopigment-a concentrations were determined from fluorescence readings on a Turner 111[2] Fluorometer before and after acidification of 24 h extractions in 90% aqueous acetone of material retained on Whatman GF/C glass filters after filtration of 140 mL water samples.

Particles

Particle concentration and size distribution (16–160 μm equivalent diameters) were determined with a Coulter model Ta counter with a 280 μm pore configured to count particles in a 20–200 mL sample volume. Counts usually exceeded 40,000 per sample. These determinations stopped part way through the study owing to equipment malfunction at the second site.

Microplankton

Microplankton samples were aliquoted prior to counting. A 0.5 mL Stempel pipette was used 10–40 times to withdraw a subsample from the well-stirred original sample after adjusting the original volume to 750 mL. When 10 Stempel subsamples yielded too many plankters to enumerate, the sample was divided with a Folsom splitter to yield a countable fraction from at least 10 Stempel subsamplings.

Microplankton samples were enumerated in covered chambers with a Wild dissection microscope (at 250 magnification) to determine mean concentrations of larval anchovy food organisms in the upper 50 m. Food organisms are here assumed to be those having ingestible dimensions (20–160 μm width), no pronounced spines or processes that would interfere with ingestion or with gut wall integrity, and, except for ingestible eggs, some degree of motility (Rojas de Mendiola 1974; Arthur 1976). Food concentrations and rations given here are underestimated because larvae are known to take organisms smaller than were retained by the meshes of the 75 μm mesh net used (Rojas de Mendiola 1974; Arthur 1976). The sampled food fraction probably represents the major part of available food rations; although less in number, this fraction is greater in volume than the unfiltered fraction and is captured selectively by larvae (Lasker and Zweifel 1978; Theilacker and Dorsey 1980). The food retained by the net is assumed here to be the majority of, and proportional to, the total rations available to larvae over the 50 m layer sampled.

Zooplankton

Zooplankton counts were made on all organisms collected in the 333 μm mesh vertical tows. Samples were not aliquoted. The net tow method used precluded quantitative representation of faster or rarer organisms, including some types of potential predators on fish larvae. Determined for each sample were number of species, number of specimens of each species, and sex ratios (where applicable) for the following major tax-

[1]K. Bliss, Oceanographer, Southwest Fisheries Center, La Jolla, CA, 92038, pers. commun. May 1985.

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

onomic groups: Medusae, Siphonophorae, Ctenophora, Chaetognatha, Cladocera, Ostracoda, Amphipoda, Copepoda, Euphausiidae, crustacean larvae, other invertebrate larvae, pelagic Mollusca, Polychaeta, Tunicata, Radiolaria, and Foraminifera. Anchovy eggs and larvae, sized to the nearest 0.25 mm, were also enumerated from these collections. Zooplankton enumerations are given in detail in Alvariño and Kimbrell (1987).

Larval Characteristics

Larval Growth

Growth of larvae was estimated from 224 larvae collected in 15 tows at Site 1 and from 116 larvae collected in 30 tows at Site 2. Samples for otolith ageing of larval anchovies were taken from the portside net of bongo tows and were preserved after removal of gelatinous zooplankters in 80% ethanol buffered with 20 mM tris [hydroxymethyl] aminomethane. Larvae were sorted from the plankton and stored in the same preservative.

Standard lengths of larvae were measured prior to removal of their otoliths. Preserved standard lengths were converted to live lengths using a correction factor for net shrinkage (Theilacker 1980). At Site 1, tow duration was six minutes and each sample was fixed within five minutes of tow completion. Length of the inshore larvae were corrected by a net shrinkage factor of eight minutes. Tow duration at Site 2 was also six minutes, but because of the large number of salps collected offshore, time before preservation increased to about 10 minutes. Lengths of offshore larvae were corrected for 13 minutes of net shrinkage.

Daily increments in the otoliths were counted using a compound microscope equipped with a closed-circuit television system, a video coordinate digitizer, and a microcomputer (Methot and Kramer 1979). Age from hatching was determined from the number of daily rings in the otoliths. Because the initial ring is deposited at the time of first feeding, at about five days from hatching, time since hatching is 5 days more than the ring count (Brothers et al. 1976).

Laird-Gompertz growth curves were fit to the length at age using nonlinear regression. To compare differences in growth rates between the two sites, analysis of covariance was performed on segments of the data so that the assumption of linearity was reasonable.

Larval Production and Mortality

Age-specific larval anchovy production rates were computed from counts of larvae in 1 mm size classes to 9 mm preserved standard length (SL) from bongo tows and in 0.5 mm size classes to 7 mm SL from CalVETs. Counts of larvae were corrected for volume of water filtered, for net avoidance, and for losses owing to extrusion through the net meshes (Zweifel and Smith 1981). Larval production at each age was estimated by dividing size-specific larval abundance by time spent at each size. Duration at size was specfied from Laird-Gompertz growth curves (Methot and Hewitt 1980; Lo 1983).

Larval mortality curves were based on the Pareto decay function (Lo 1985):

$$z(t) = \beta/t$$

where $z(t)$ is the instantaneous mortality rate (IMR), β is the IMR coefficient, and t is age (days) since spawning. Daily production is given by

$$P_t = P_0(t/t_0)^{-\beta} \quad t_0 < t < 20\ d$$

where P_t is daily larval production at age t, P_0 is initial larval production (at hatching), t_0 is age at hatching, specified from hatching time as a function of incubation temperature (Lo 1983). Thus, as larvae grow older, the rate at which they appear in the next age group is diminished by the factor given by β.

The above equation (referred to subsequently as the nonlinear model) can be expressed in linear form by taking the natural logarithm of both sides:

$$\ln(P_t) = \ln(P_0) - \beta \ln(t/t_0)\ .$$

Both the nonlinear and the log-linear regression models can be used to estimate parameters P_0 and the IMR coefficient β. The log-linear equation is mainly used in this study to compare β between sites.

Production and mortality of anchovy larvae at Site 1 were estimated from 48 bongo samples (20 using 333 μm mesh nets and 28 using 505 μm mesh nets) and from 49 CalVETs using 150 μm mesh nets. At Site 2, these parameters were estimated from 49 bongo samples using 505 μm mesh nets and from 50 CalVETs using 150 μm mesh nets.

Larval Condition

Starvation incidence was estimated from histological criteria on 141 anchovy larvae from Site 1 and on 119 larvae from Site 2. The larvae were collected with nonquantitative bongo nets towed to 50 m. Although the best preservation procedure for histological samples is to preserve larval fish in Bouin's fixative within 3 minutes after capture, 5–6 minutes were required to obtain representative samples to 50 m. After fixing in Bouin's fluid for 24–48 hours, samples were transferred to 70% ethyl alcohol for storage.

The nutritional state of northern anchovy larvae is usually classified by grading the appearance of tissues of the brain, cartilage, notochord, liver, pancreas, and gut (O'Connell 1976). But because many of these tissues had lysed owing to extended time before preservation, an additional criterion was used in this study. This criterion, the height of midgut mucosal cells, was unaffected by the 5–6 minutes needed to fix the larvae (Theilacker and Watanabe 1989). Heights of midgut mucosal cells were divided into three categories (healthy, intermediate, and starved) according to laboratory results (Theilacker and Watanabe 1989). As northern anchovy develop past 6 mm SL, the midgut folds to increase the absorptive area. The fold makes it difficult to measure cell heights of larger larvae. To apply the durations determined for the laboratory fish to the field samples, the size of the field-collected larvae was adjusted to equal the size of preserved laboratory fish of known feeding history (Theilacker 1980). Details of these manipulations are given in Theilacker and Watanabe (1989).

RESULTS

Environmental Variations Within and Between Drifters and Sites

Surface Drift

Drifters were tracked as shown in Figure 2. Released 10 nmi apart at Site 1, Drifters A and B moved generally eastward, away from Santa Catalina Island, on slightly convergent courses. Mean speeds over their 2.7 days at sea were 17.1 cm/s and 18.7 cm/s (about 15.5 km/dy). Range of speeds measured by drifter displacements over 8 h intervals were 5.6–34.7 cm/s and 6.8–32.9 cm/s.

Released 5 nmi apart at Site 2, Drifters A and B moved in a southeast-trending arc, again on slightly convergent courses. Mean speeds over their 2.5 days at sea were 34.6 cm/s and 37.4 cm/s (about 30 km/d), twice as fast as at Site 1. Speed ranges measured were 15.3 cm/s to 45.4

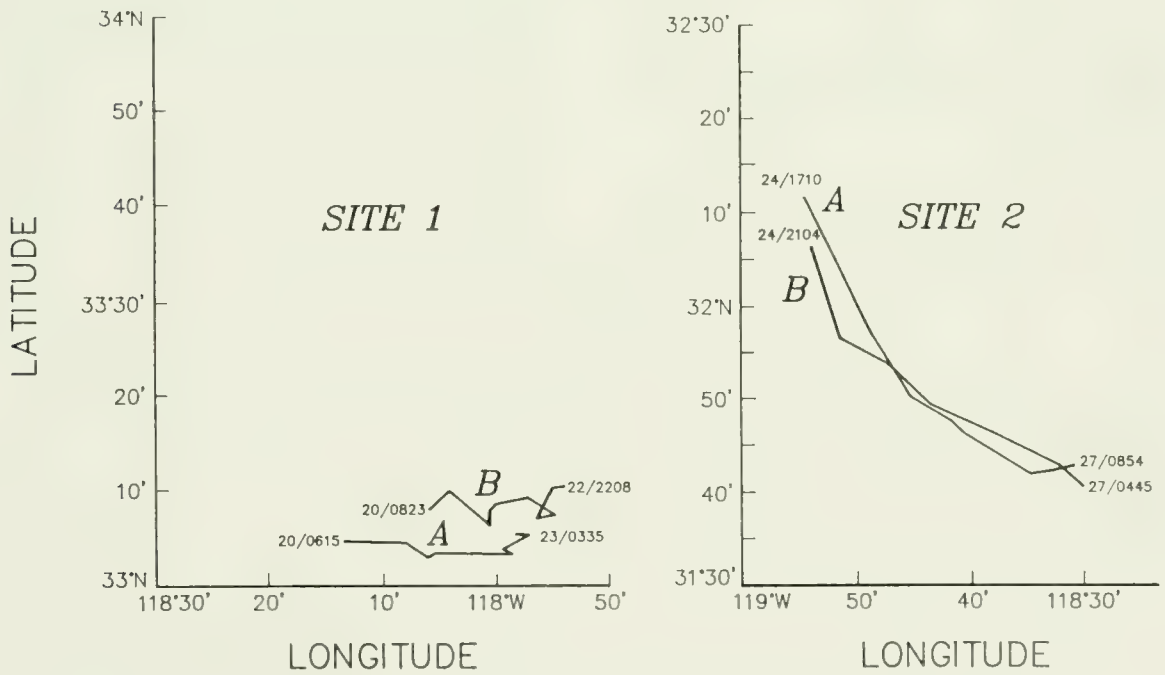
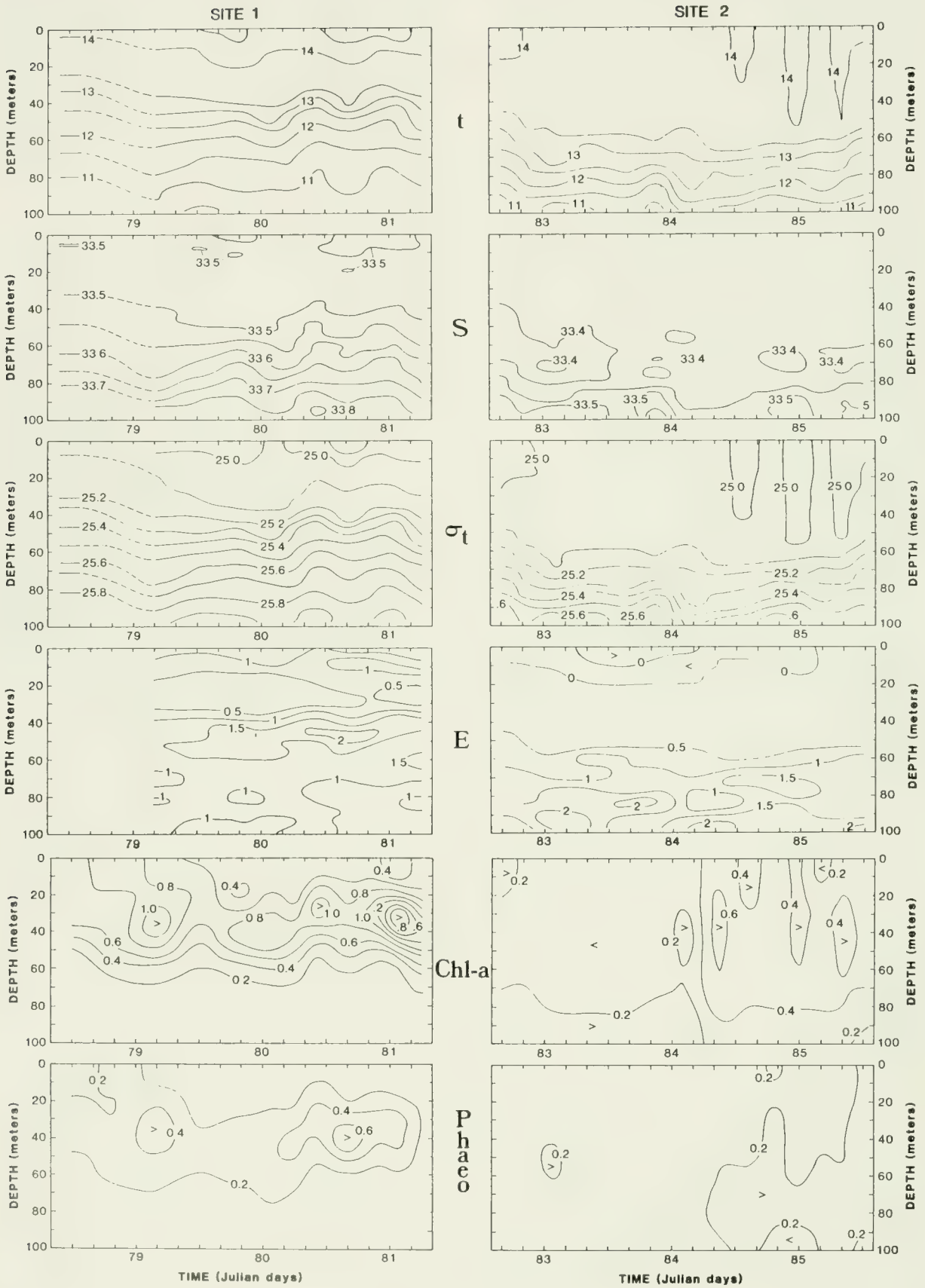


FIGURE 2.—Drifter trajectories along *Sites 1* and *2*.


SITE 1
SITE 2
t
S
σ_t
E
Chl-a
Phaeo
DEPTH (meters)
TIME (Julian days)

cm/s and 18.8 cm/s to 48.2 cm/s. Drift direction at Site 2, predominantly longshore, indicated that Site 2 larvae had been spawned offshore rather than drifting out from an onshore spawning area.

The degree to which drifter displacements paralleled one another at each site (Fig. 2) indicated homogeneous, nondivergent flow of the surface layer and general integrity of each water corpus being investigated. Similar rates of separation of drifter pairs indicated no differences between rates of lateral diffusion between sites.

Vertical Structure

Physical structure of the upper 100 m at both sites exhibited no overall trends for the duration of the study (Fig. 3). Variations of isopleth depths in the pycnocline at Site 1 were greater during the second half of the period, perhaps owing to increased internal wave activity.

A slight warming trend over the course of the studies was indicated by increased surface layer temperatures at both sites. The trend was likely due to local heating of the mixed layer. Heat content of the upper layer increased at Site 2 but no trend was detected at Site 1.

Local diurnal heating was apparent at Site 1 from continuous temperature records at 3 m depth as well as from CTD casts. Higher winds and a thicker mixed layer at Site 2 obscured diurnal temperature variations.

Vertical sections of phytopigments (Fig. 3) gives a less conservative picture of variations. Intensification of the maximum chlorophyll and phaeopigment layers over the course of studies occurred at both sites. In view of the lack of change of temperature, salinity, and density structure, the increase in pigment concentration was likely due to local processes rather than to advective processes. The change thus expressed the net product of primary production and grazing.

Composite T-S diagrams (Fig. 4), constructed from CTD cast data at each site, indicate that the drifters were set into waters of different structure and composition at the two sites. Site 2 water, closer in character to California Current core water (Lynn and Simpson in press), was cooler and less saline than Site 1 water. Site 1 water was likely derived from a mix of California Current core water (from the north, offshore) and coastal countercurrent water (from the south, nearshore), further modified by local warming of the surface layers in transit.

Plankton Quantity and Composition

Within sites, no major differences were apparent in plankton quantity or community composition along drifter paths. Over twice as many plankton organisms were caught by 333 μm mesh nets at Site 1 than at Site 2, and predatory copepods were 5 times more numerous at Site 1 than at Site 2 (Table 1). Plankton diversity was somewhat higher at Site 1 than at Site 2: on average, Site 1 tows yielded 144 invertebrate species, whereas Site 2 tows yielded 130 species. Perhaps the most striking difference in the zooplankton was the high abundance of salps at Site 2. No direct interactions are known between fish larvae and salps.

In terms both of rations and numbers, over twice as much larval anchovy food was caught by 75 μm mesh nets at Site 1 than at Site 2 (Table 1).

Summary

To compare habitats at the two sites, Table 1

[3]Lynn, R. J., and J. Simpson. 1989. The influence of bathymetry upon the flow of the undercurrent off Southern California. Unpubl. manuscr.

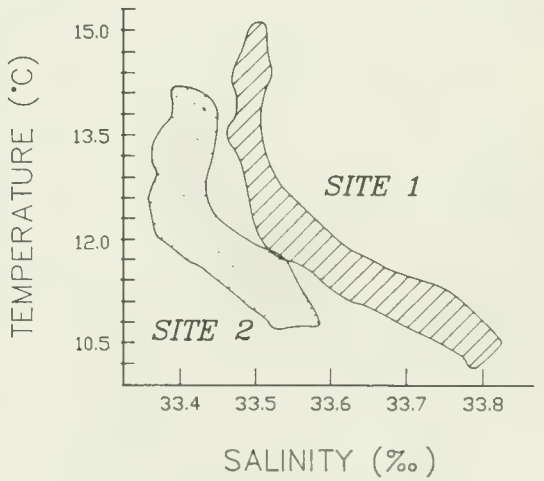


FIGURE 4.—Composite T-S diagrams at *Sites 1* and *2*.

FIGURE 3.—Vertical time sections of temperature (t), salinity (‰), density (σ_t), and stability (E) at Sites 1 and 2. Vertical time sections of chlorophyll-a and phaeopigment at Sites 1 and 2.

TABLE 1.—Comparisons between study sites—means (and standard deviations) of environmental characteristics at Sites 1 and 2. *n* is number of observations. Integrations are to 50 m depth.

	Site 1		Site 2	
	mean (SD)	*n*	mean (SD)	*n*
mixed layer depth (m)	37.6 (5.0)	11	57.7 (6.8)	14
wind speed (m/s)	3.27 (1.54)	15	8.97 (2.36)	14
stability max. ($E \times 10^7$)	4.00 (1.54)	11	3.47 (1.59)	14
depth of stability max. (m)	45.6 (7.8)	11	67.6 (8.7)	14
surface current speed (cm/s)	18.9 (10.2)	16	35.4 (10.4)	16
surface temp. (C)	14.50 (0.41)	50	14.04 (0.14)	50
surface salinity ‰	33.50 (0.011)	11	33.42 (0.044)	14
surface chlorophyll a conc. (μg/L)	0.56 (0.20)	11	0.37 (0.15)	12
surface phaeopigment conc. (μg/L)	0.14 (0.13)	11	0.10 (0.09)	12
integrated chlorophyll a conc. (mg/m^2)	45.3 (9.74)	11	33.8 (12.72)	12
integrated phaeopigment conc. (mg/m^2)	20.3 (4.77)	11	15.9 (7.64)	12
Integrated particle conc., 16–160 μm (no/cm^2)	44012 (44761)	11	66980 (67027)	5
Integrated particle conc., 50–160 μm (no/cm^2)	5854 (9405)	11	2607 (1138)	5
Secchi depth (m)	11.5 (2.0)	9	18.1 (2.7)	8
food conc. >75 μm (no/L)	31.4 (13.9)	26	13.5 (12.0)	24
food conc. >75 μm ($\mu m^3/L$)	19.6 (5.7)	26	8.1 (7.0)	24
zooplankton conc. (no/m^3)	625 (216)	26	236 (160)	24
predatory copepods (no/m^3)	121 (79)	26	24 (32)	24
zooplankton spp. (species/tow)	144	26	130	24
copepod spp. (species/tow)	65	26	60	24

gives means and variations among environmental parameters of energy input and dissipation, responses of the plankton communities, and levels of food supply and predation pressure to which the larvae were exposed. Analyses of variance of environmental characteristics demonstrated much smaller variations between drifters within sites than between sites.

In review, changes over study periods at both sites were local, not advective; we resampled the same water and larval population within sites. Vertical gradients were shoaler and more intense at Site 1. Temperature and salinity relations in the upper 100 m indicate different recent histories of the waters at the two sites. Surface layers at Site 1 were warmer, more saline, less turbulent, less transparent, and contained higher concentrations of larval foods and other

plankton. Plankton community structure was different between sites: most notably, predatory copepods were more abundant at Site 1 and salps were more abundant at Site 2.

Larval Parameter Variations Within and Between Drifters and Sites

Larval Growth Rates:

Ranges of size and age of larvae differed between sites. Site 2 samples included larvae that were larger (and older) than those at Site 1. The average age of larvae was 6.9 and 11.5 days from hatching at Sites 1 and 2, respectively. Larval length averaged 7.8 mm and 9.0 mm at Sites 1 and 2, respectively. Thus the offshore Site 2 was inhabited by older and slightly longer larvae than Site 1. Offshore drift of larvae hatched inshore into the region of Site 2 (Smith 1972) may account for this phenomenon, as may higher predation on older larvae at Site 1. The latter explanation is favored because the observed flow patterns (Fig. 2) do not suggest that larvae were transported offshore from nearshore areas.

To assess the growth of larvae in these two stations, the Laird-Gompertz model was used to fit the length-age data:

$$L_t = L_\infty (L_0/L_\infty)^{\exp[-\alpha t]}$$

where t is time since first feeding at 5 days after hatching, L_0 is larval length at first feeding, and L_∞ is the asymptotic length. The maximum and minimum fish lengths in the sample have strong influence on the length parameter estimates (L_0 and L_∞) and on the growth coefficient (α). The resulting growth coefficients at the two sites (Table 2) are 0.1 for the inshore station and 0.05 for the offshore station. A standard growth coefficient of 0.05 is used by CalCOFI (Methot and Hewitt 1980).

We compared total growth rates of fish younger than 18 days (after hatching) at the two sites, assuming a linear growth rate to be reasonable because of difficulties in comparing differences between nonlinear curves. Larvae at the offshore Site 2 had a larger asymptotic length and a lower growth coefficient than at the inshore site. The null hypothesis, that growth was equal at the two sites, was tested using analysis of covariance. When the test was performed on lengths uncorrected for shrinkage or on lengths corrected for the same shrinkage, the slopes at the two sites were not significantly different but the mean lengths were. (A true difference between mean lengths would indicate that anchovy larvae had hatched at a larger size at Site 1 than at Site 2, or that Site 2 larvae underwent starvation at the first-feeding stage and then recovered.) However, when larval lengths from Site 2 were corrected for greater handling time, then neither the slopes nor the adjusted lengths differed significantly between the two sites (Table 3). In short, corrected data indicate that no difference existed in larval growth between the sites.

Larval Production and Mortality Rates

Larval production at age (larvae <20 days from spawning) was used to model larval mortality. For mortality analysis, age is defined as time since spawning. Larval production was computed as described above in Methods, and larval age was derived from live size using a Gompertz growth curve. Three growth curves were available for computing larval age: the standard growth curve used for routine annual anchovy larval assessment, and two site-specific growth curves constructed from length-age data collected at each of our sites. We elected to use the standard growth curve to convert larval size to age for both sites because no significant difference in total growth rates for larvae <20 days since spawning was detected between two site-specific growth curves, and because the growth coefficients estimated from two sites were also similar to that of the standard growth model (all equal to 0.05) when the maximum and minimum lengths of larvae were set to be 27 mm and 4.1 mm, corresponding to the standard growth curve. Both nonlinear and log-linear regression

TABLE 2.—Parameters of Laird-Gompertz growth curves for northern anchovy larvae at Site 1 and Site 2. L_0 is larval length at first feeding; L_∞ is the asymptotic length; and α is the growth coefficient. Lengths are corrected for differential handling times.

Parameter	Site 1	Site 2	CalCOFI
L_∞ (mm)	14.7 (0.6)	20.5 (1.8)	27
L_0 (mm)	4.9 (0.1)	5.2 (0.2)	4.1
α	0.10 (0.01)	0.05 (0.01)	0.05
n	234	141	—
With L_∞ (mm) fixed at 27 mm and L_0 (mm) fixed at 4.1 mm,			
α	0.05 (0.001)	0.05 (0.01)	

TABLE 3.—Comparison of growth rates of northern anchovy larvae between Site 1 and Site 2 for post-yolk-sac larvae less than 18 days old, using analysis of covariance.

Linear regression of growth. L is length, t is time since hatching, and n = total number of larvae sampled.

Site 1	$L_t = 7.33 + 0.46\ (t - 9.99)$	$n = 197$
Site 2	$L_t = 7.82 + 0.46\ (t - 11.54)$	$n = 79$

Analysis of covariance between sites

Source of variation	df	Sum of squares	Mean squares	F	Prob. (tail)
Equality of adjusted means	1	2.57	2.57	3.23	0.07
Zero slopes					
All covariates	1	709.76	709.76	892.98	0.00
error	273	216.99	0.79		
Equality of slopes all covariates and all groups	1	0.02	0.02	0.02	0.89
error	272	216.97	0.80		

were used to estimate the larval production at hatching (P_0) and mortality coefficient (β).

Mortality Estimates

Data in three arrays were used to estimate mortality: bongo larvae alone, bongo larvae plus 2.5–4.0 mm larvae from CalVETs, and bongo larvae plus 3.0–4.0 mm larvae from CalVETs (Tables 4, 5). The nonlinear regression gave estimates of β ranging from 1.15 to 2.18 (equivalent to IMR of 0.115–0.218 for larvae of age 10 days) for Site 1 and 1.06–3.03 for Site 2. The lower values of β were caused by low numbers of 2.5 mm larvae in CalVET samples. The log-linear regression produced more consistent estimates of β than those from nonlinear regression: Site 1 values ranged from 3.32 to 3.94 and Site 2 values ranged from 2.87 to 3.47. Estimates of P_0 at hatching age ranged at Site 1 from 12.03 to 28.38, and for Site 2 from 1.37 to 4.23. For all data arrays, site differences in larval production rates were apparent (Tables 4, 5), but site differences in mortality rates were not (Table 6).

Comparison of Larval Production and Mortality Coefficients Between Sites

Larval samples from bongo tows were used to compare the mortality between sites. Analysis of covariance was performed on the logarithmic transformation of age and larval production. The results of the analysis indicated that the site difference between mortality coefficients was not statistically detectable whereas site difference between larval production rates was (Table 6).

We also compared the larval production and mortality at the two sites (Table 5) with those over the northern anchovy spawning domain as sampled by the CalCOFI 8502 survey ($P_0 = 4.81$ with SE = 0.30, and $\beta = 2.21$ with SE = 0.11 for 37 positive CalVET tows out of 45). Larval production at Site 1 was much higher than the average over the CalCOFI 8502 survey region, but production at Site 2 and larval mortality at both sites were similar to the survey region averages.

Figure 5 shows the larval production-at-age curves at the two sites and, for comparison, larval production curves for anchovy spawning domains as sampled on CalCOFI Cruise 8502, just prior to our site-intensive program. Site 1 displayed high production of all larval ages, which was higher than its subdomain (CalCOFI Region 7), whereas Site 2 production was somewhat above that of its subdomain (CalCOFI Region 8) and somewhat below that of the entire spawning domain as sampled ("all regions").

Starvation Incidence

Midgut cell height is the histological criterion of larval feeding history. The range of cell height and the cell height change with larval size were similar at both sites (Fig. 6). The similarity

TABLE 4.—Northern anchovy larval production per unit area per day at age at Sites 1 and 2 from bongo and CalVET nets, based upon "regular" growth. *n* is total number of tows, pos. *n* is number of tows with larvae.

Capture size (mm)	Site 1 Average age (d)	Site 1 Production no./0.05 m^2/d	Site 2 Average age (d)	Site 2 Production no./0.05 m^2/d
Bongo net				
2.5	4.72	10.67	5.29	0.95
3.75	8.30	5.57	9.20	0.19
4.75	11.04	0.54	11.91	0.074
5.75	13.44	0.16	14.38	0.033
6.75	15.64	0.096	16.69	0.024
7.75	17.78	0.085	18.86	0.022
8.75	19.84	0.095	21.06	0.016
n(pos.*n*)	48 (48)		49 (46)	
CalVET net				
2.5	3.60	6.44	3.81	0.674
3.0	5.09	7.81	5.37	1.221
3.5	7.16	7.65	7.56	1.503
4.0	8.90	3.19	9.27	0.445
4.5	10.10	0.27	10.50	0.098
5.0	11.41	0.44	—	—
5.5	12.86	0.04	—	—
6.0	13.38	0.04	—	—
6.5	14.78	0.02	—	—
n(pos.*n*)	49(49)		50(40)	
temperature	14.25C		14.05C	
hatching age	3.05d		3.23d	

[1]Production computed from total number of tows(n).

TABLE 5.—Estimated northern anchovy larval production at hatching (P_0) and mortality coefficient (β) from nonlinear and log-linear regression for Sites 1 and 2 using various data sets and "regular" growth parameter estimates.

Data sets	Site 1 P_0 (SE)	Site 1 β (SE)	Site 1 MSE	Site 2 P_0 (SE)	Site 2 β (SE)	Site 2 MSE
Nonlinear bongo only	28.38 (7.70)	2.18 (0.47)	1.78	4.23 (0.15)	3.03 (0.07)	0.0008
CalVET (2.5–4.0 mm) and bongo	12.03 (2.98)	1.15 (0.38)	6.01	1.37 (0.51)	1.06 (0.52)	0.1816
CalVET (3.0–4.0 mm) and bongo	23.79 (5.86)	1.85 (0.38)	2.47	2.99 (1.40)	1.80 (0.68)	0.1238
Log-linear bongo only	4.49 (0.77)	3.9 (0.54)	0.43	1.41 (0.22)	3.05 (0.15)	0.03
CalVET (2.5–4.0 mm) and bongo	3.79 (0.59)	3.32 (0.48)	0.74	1.36 (0.52)	2.87 (0.42)	0.57
CalVET (3.0–4.0 mm) and bongo	4.67 (0.58)	3.94 (0.45)	0.46	2.22 (0.49)	3.47 (0.38)	0.31

suggests that both larval populations had experienced comparable feeding conditions.

Although average daily mortality rates due to starvation of first-feeding anchovy larvae were higher at Site 1, 24%/d, than at Site 2, 12%/d (Table 7), the difference between sites was not statistically significant ($\chi^2 = 2.26$; $P > 0.15$). Incidence of starvation was low or nil after the first-feeding stage at both sites.

TABLE 6.—Comparison of mortality coefficients (β) of northern anchovy larvae (<20 days) between Site 1 and Site 2, using analysis of covariance. P_t is the larval production at age t; t is age (d) from fertilization. The values 3.05 and 3.23 are ages at hatching.

Log-linear regressions of mortality are

Site 1 $\ln(P_t) = 4.49 - 3.90\ [(\ln(t/3.05))]$

Site 2 $\ln(P_t) = 1.4 - 3.05\ [(\ln(t/3.23))]$

Analysis of covariance between sites

Source of variation	df	Sum of squares	Mean square	F	Prob. (tail)
Equality of adjusted means	1	13.26	13.26	50.90	0.00
Zero slopes					
All covariates	1	35.12	35.12	134.80	0.00
error	11	2.87	0.26		
Equality of slopes all covariates and all groups	1	0.52	0.52	2.24	0.17
error	10	2.34	0.23		

DISCUSSION

We had expected to find higher rates of larval northern anchovy growth and survival in the inshore than in the offshore environment. Bias or low precision cannot explain the similarity of growth and mortality coefficients between sites. The larval anchovy parameters might have been biased had we sampled larval populations imported from other sources by advection or diffusion over the course of the measurement periods, but our time series of environmental characteristics display no shifts to indicate short-term change of properties or of populations at the drifters. Similarly, lack of precision cannot be invoked: the number of tows and larvae were sufficient to distinguish mortality coefficients (β) differing by 0.5 with an 86% probability (Lo et al. 1989). We must accept that the mortality coefficients were and that many more similar tows would be necessary to distinguish between them.

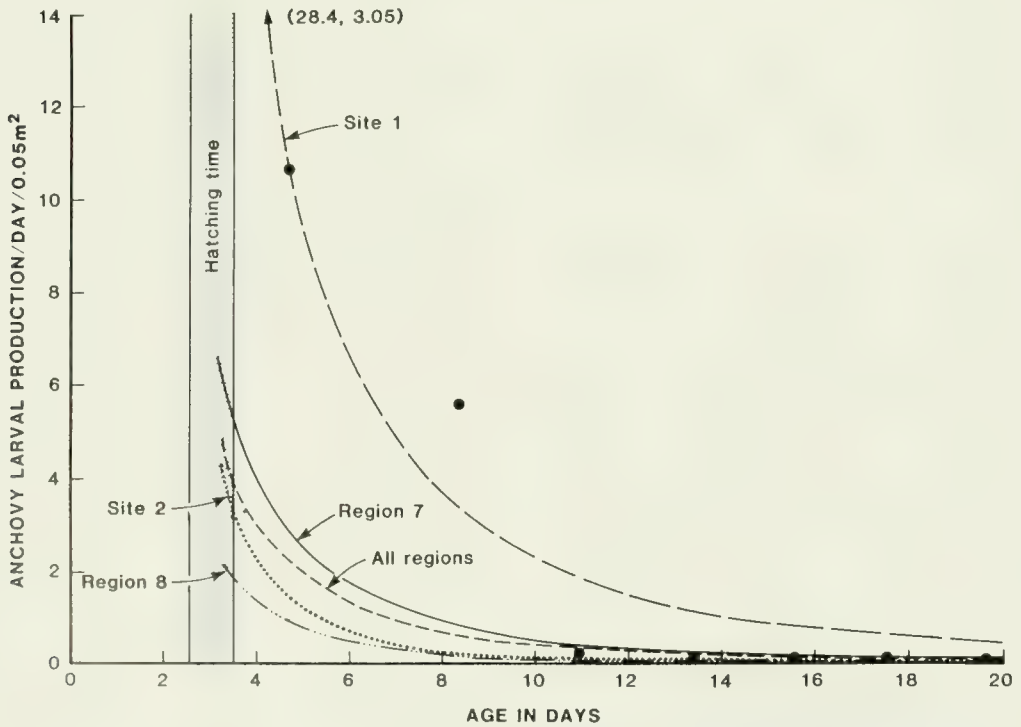


FIGURE 5.—Daily larval production vs. age for northern anchovy and fitted larval mortality curves for Site 1 and Site 2, and for CalCOFI 8502 survey and subregions. Points are for Site 1 only.

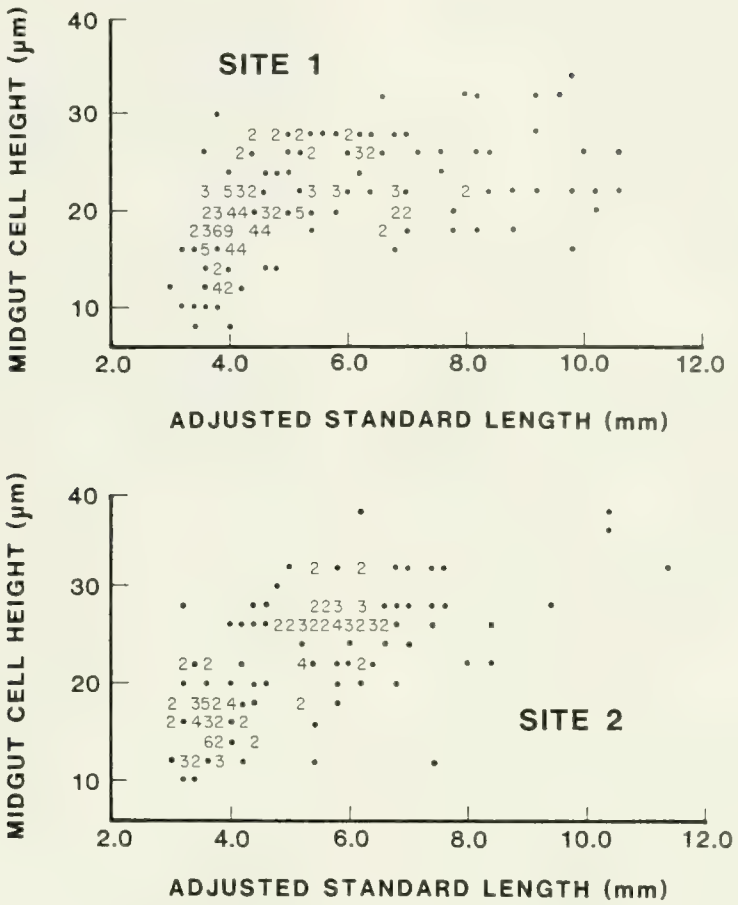


FIGURE 6.—Midgut cell heights of individual northern anchovy larvae collected at Site 1 (inshore) and at Site 2 (offshore).

TABLE 7.—Histological condition of larval northern anchovy at Sites 1 and 2. *n* = number examined; dur = duration; *n*/d = number/day; S = starved; I = intermediate; H = healthy; %/d = % dying/day due to starvation.

	Site 1					Site 2				
	S	I	H	total	%/d	S	I	H	total	%/d
3–4 mm (SL)										
n	9	17	28	54		4	32	21	57	5
dur	2	5	2.5			2	5	2.5		
n/d	4.5	3.4	11.2	19.1	24	2.0	6.4	8.4	16.8	12
4–5 mm (SL)										
n	1	11	48	60		0	5	20	25	
dur	2	3	2.5			3	3	2.5		
n/d	0.3	3.6	19.2	23.1	1	0	1.7	8	9.7	0
5–6 mm (SL)										
n	0	0	27	27	0	0	2	35	37	0
Total number examined				141					119	

Similarity of growth and starvation indices at the two sites indicates that most larvae had encountered sufficient forage to sustain "normal" growth rates, or that the fraction that had not done so were quickly removed from the system, i.e., not represented in our collections. Food abundance estimated from integrative tows may not reflect the actual availability of food to larvae because microplankton prey frequently occur in patches and laminae of very small extent (cf. Owen 1989). Also, larvae may have been sustained on food that passed through the net. Fewer larvae were collected at Site 2 than at Site 1, but starvation incidence was at least as low there as at Site 1. Furthermore, Site 2 larvae were growing as fast as those at Site 1, even though average microplankton concentration at Site 2 was less than half that at Site 1. Despite lower average food concentrations, there were zones at Site 2 that evidently contained enough food to support growth of the larvae.

An analogous result is given by Butler (1989), which showed that periods of diminished forage production, such as el Niño, have no discernible effect on growth rates of field-caught larvae. But Theilacker and Watanabe (1989) showed by experiment that starvation measurably retards larval growth. This apparent paradox is resolved if, in the sea, larvae that survive to be sampled have found enough food to grow at normal rates even in abnormal periods, whereas larvae that have been deprived to the extent that their growth is adversely affected soon vanish, perhaps by predation owing to their weakened condition rather than by starvation directly.

In contrast with the common view that northern anchovies broadcast sex products indiscriminately with the strategy that some get lucky, we advance the hypotheses that anchovy spawn where their offspring are equally likely to survive, even under widely different environmental conditions, and that these conditions mediate their spawning intensity. This is the central theme of MacCall's (1983) "Basin Model" of habitat selection by the northern anchovy.

The Basin Model postulates that when a population is large, its adults occupy less suitable habitats in which mortality of spawn per capita tends to equal that in more favorable habitats. This occurs because cannibalism of spawn by adults is higher in favored habitats than in peripheral habitats.

We roughly partition sources of overall larval mortality (β_t) into that due to cannibalism (β_c) and that due to other causes (other predation, β_p, and starvation, β_s). Diffusive change, a source of "apparent" mortality, is assumed from physical arguments above to be the same at both sites. Thus,

$$\beta_t = \beta_c + \beta_p + \beta_s .$$

If higher egg concentration denotes higher adult occupation, β_c was greater at Site 1 than at Site 2. Anchovy egg concentration at Site 1 averaged $37/m^3$, 15 times the egg concentration at Site 2. This difference is too great to be attributed to differences in batch fecundity of the spawners, which varies by a factor of about two (Hunter et al. 1985).

For larval mortality, β_t, to have been equivalent at the two sites, mortality from other sources ($\beta_p + \beta_s$) is required to have been greater at Site 2 than at Site 1 to the degree of offsetting the difference between sites in parental consumption of spawn (β_c). But neither larval growth rates nor starvation incidence differed between sites, showing that their β_s values were about equal. This being so, cannibalism was offset by other predation rather than by starvation. This requires increased predation (β_p) at Site 2 over that at Site 1.

For comparison of β_p between sites, we formed rough indices of predation pressure, P, from catches by vertical net tow pairs. P is the concentration of the five most numerous predators caught by the 333 μm mesh net, divided by concentration of anchovy eggs and larvae caught in the corresponding 150 μm mesh net. Predator populations in the samples consisted mainly of raptorial copepods and chaetognaths. Mean values of P were 2.8 predators/anchovy at Site 1 (26 tows) and 5.5 predators/anchovy at Site 2 (24 tows). This difference indicates compensatory predation at Site 2. Confirmation of compensatory predation, however, is not possible from this data set because our nets missed larger, faster predators such as euphausiids, and because species-specific and size-specific predation rates are largely unknown.

CONCLUSIONS

Among the several characteristics of the ichthyoplankton investigated at contrasting habitat sites, only one, larval production rate, was clearly different between sites. Growth and

mortality rates were statistically indistinguishable between sites. Mortality due to starvation was about the same at the two sites. Larval production at Site 1 was well above the CalCOFI survey average, but Site 2 production and larval mortality at both sites were similar to those over the entire CalCOFI region.

Habitat characteristics at the two sites differed substantially. Site 1 was relatively eutrophic, as seen by its high concentrations of larval forage, zooplankton, chlorophyll, and phaeopigment. Site 2 was much more energetic, as seen by its greater wind speed, current speed, mixed layer depth, and depth of maximum stability. With the exception of predatory copepod abundance, every measured characteristic of the environment favored larval anchovy well-being more at Site 1 than at Site 2.

Yet the well-being of anchovy larvae was about the same at the two sites. Anchovies spawned under conditions where their larvae could grow and survive at about the same rates, despite the differences noted in the respective environments. Similar larval growth rates and the low incidence of starving larvae indicate adequate forage availability in both habitats. In agreement with MacCall's (1983) Basin Model, rates of larval anchovy mortality at the two sites were not greatly different and the same fraction of the original larval production survived to the schooling stage.

We consider this work to be a pilot effort to stimulate and guide research that we hope will be more experimental in scope and execution. To test our hypotheses, environments that more completely span the "suitable basin" need to be described and occupied long enough to follow characteristics of larval fish cohorts from egg to metamorphosis.

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Abalone (Genus *Haliotis*) Mariculture on the North American Pacific Coast

David L. Leighton

ABSTRACT: First commercial attempts to culture native Pacific coast abalones were undertaken in California in the mid-1960s. These pioneering groups established basic techniques and stimulated the development of a half-dozen abalone production operations, still chiefly in California. Refinements to the culture technology have resulted from research and development by the industry, but also through studies conducted by nonprofit research groups and government and university programs. This paper briefly examines recent trends in world abalone fisheries and the requirement for mariculture, then describes and evaluates the principal elements contributing to the technological advancement of abalone mariculture in North America.

Substantial advances have been made in the artificial propagation of members of the genus *Haliotis* during the past two decades in the United States, Japan, Australia, New Zealand, and France. Faced with the necessity to supplement the fishery catch or to avert anticipated declines in supplies of this valuable marine resource, efforts in several countries are being directed toward development of effective hatchery programs for production of juvenile stock for use directly in fishery enhancement (through seeding) or for grow-out and production by mariculture. Profit incentives alone have spurred the evolution of private sector intensive abalone culture in the United States.

By far the greatest national effort to increase abalone production has occurred in Japan. Over 30 fisheries laboratories and "Fisheries Farming Centers" throughout that country are concentrating efforts on generation of juvenile abalone (seed) for release in the sea (Uki 1981; McCormick and Hahn 1983). Collectively, these facilities produce about 30 million seed annually (Uki 1981; Grant 1981). Authoritative reviews are also provided by Ino (1980) and Saito (1984).

The Pacific abalone, *Haliotis discus hannai*, is the primary species cultured in Japan, China, and Korea (Sheehy and Vik 1981). Recent attempts to culture the pauas (chiefly *H. iris*) in New Zealand (Anon. 1986) as well as *H. ruber and H. laevigata* in Tasmania (D. Cropp 1987[1]) are showing encouraging results. The ormer, *H. tuberculata*, is being produced in initial programs in Britain and France (Flassch and Aveline 1984). Other experimental and incipient commercial attempts to culture native and introduced species are in progress in Canada (Fletcher 1987), Mexico (Aguirre 1988), and Chile (Owen et al. 1984).

On the Pacific coast of the United States several species of abalones have been subjects of experimental and commercial aquaculture for almost two decades, chiefly the red, *H. rufescens*, and the green, *H. fulgens*. The red abalone is the largest member of the genus and, historically, the major fishery species. First attempts to cultivate abalone in the Western Hemisphere involved this species (Owen et al. 1971; Leighton 1977, 1987). The green abalone, native to temperate waters of southern California and northern Mexico, is broadly tolerant of temperature (Leighton 1974). Some new commercial enterprises are focusing on green abalone production to capitalize on its versatility, relatively rapid growth, and ready marketability. Until quite recently, only in the United States have abalone been cultured to adult size (5–10 cm) by intensive methods for direct marketing as seafood products. Operations elsewhere in the world have focused on producing seed for restocking programs, but it is anticipated that newly established operations for full grow-out will soon expand in Japan, Australia, New Zealand, and Canada.

STATUS OF THE FISHERY

Abalones, all in the genus *Haliotis*, are herbivorous marine gastropods which have long

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been utilized as food by man. Nearly 90 species and subspecies are recorded as living in the world today. Paleontological records indicate the presence of the genus since the Cretaceous (Cox 1962). Most extant species live in shallow waters, feeding on marine algae common on rocky substrates from the intertidal to depths over 50 m.

A staple item in the diet of coastal native American tribes, abalone have also been of major importance as food, medicine, and elements of ritual in Asia for centuries. In modern times, extensive exploitation in many countries has resulted in a marked reduction of fishery stocks. Prior to the onset of abalone population decline in California, annual harvests generally exceeded 4.5 million pounds (>2,000 t, see below). In Japan, annual yields have been over 10 million pounds, supplemented now by an intensive nationwide habitat improvement and seeding program (Uki 1981). Production, chiefly from fisheries, has exceeded 44 million pounds (20,000 t) annually (FAO 1975). Worldwide, the market for abalone and abalone products is estimated at more than $300 million (NMFS 1982[2]). Countries most productive in this fishery have been Japan, Mexico, Australia, South Africa, and the United States.

[2]National Marine Fisheries Service. 1982. Southwest Regional Headquarters, Long Beach, CA. (Unpubl. rep.)

In North America, fisheries continue to provide the major supply of abalone, although aquaculture is gaining rapidly as a significant new source, currently estimated at about 5% of the total harvest. Commercial quantities of abalones have been found chiefly along the coasts of California and northern Baja California, Mexico. A small fishery exists in Canada for the pinto abalone, *H. k. kamtschatkana*, (Mottet 1978).

Large-scale exploitation of abalones in California has been in progress for almost a century. Intertidal and shallow subtidal populations were severely depleted by Asian harvesters around the turn of the century. As diving techniques improved and the number of divers increased, especially following World War II, deep-water populations were similarly impacted (Cicin-Sain et al. 1977). An alarming decline was seen in the early 1970s, and annual harvests dropped to less than one million pounds after 1974 (Fig. 1). Comparable declines have been experienced in Mexico, Japan, and elsewhere in the world were intensive fisheries for abalones have developed. However, the demand for abalone remains strong, especially in Asian countries. Japan now imports quantities almost equal to the domestic harvest (Uki 1981).

Circumstances surrounding the decline of the California abalone populations have been unique. Red abalone, once abundant off the central California coast, supported the bulk of the commer-

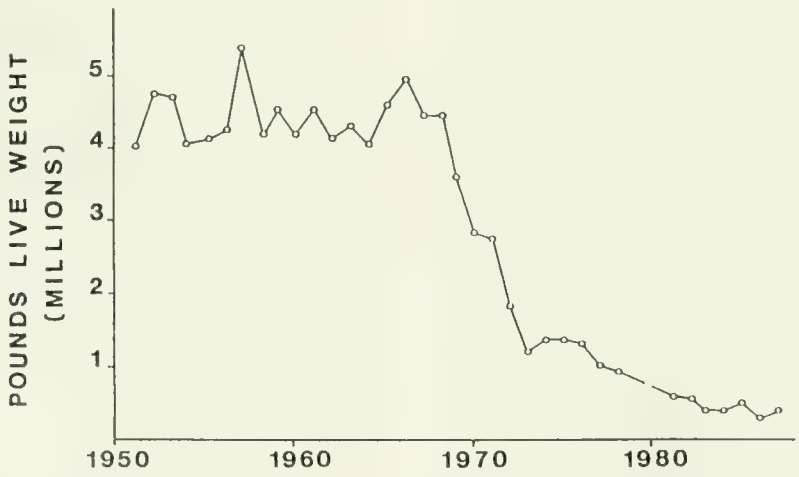

FIGURE 1.—California commercial landings for red, green, and pink abalones, 1951–87. Red abalone predominated in catch until 1975. During 1981–87 average annual landings of red abalone dropped to 329,410 pounds (in-shell) while black abalone take averaged 414,620 pounds. Data from Cicin-Sain et al. (1977) and California Department of Fish and Game, Marine Statistics, Commercial Fish Landings, 1982–87. Other records for 1976–81 from Fish Bulletin 168 and 170, and unpublished logs. Reports for 1979 and 1980 not available.

cial take until about 1965. Thereafter both the toll of increased fishing pressure and increased depredation by the rapidly expanding California sea otter populations significantly reduced red abalone stocks (Cicin-Sain et al. 1977). A combination of pollution, habitat loss, competition with uncontrolled sea urchin population growth, mortalities of undersize abalone due to "bar cuts", and increased harvests by both sport and commercial divers have had a severe impact on stocks of all species of abalones, especially in Southern California (Cicin-Sain et al. 1977). An important additional element in the decline of California abalone populations has been the establishment of seasonal closures which do not adequately protect a large portion of the breeding populations. The midwinter closure for both commercial and sport abalone harvests (mid-January to mid-March) existed for several decades. Since pink (*H. corrugata*), green, and black (*H. cracherodii*) abalones spawn from late spring to late fall (Leighton 1974; Tutschulte 1975), no reproductive protection was afforded by that measure. Only the deep-water, late-winter to spring spawning white abalone, *H. sorenseni*, and a fraction of the year-round spawning red abalone populations, were benefitted by the California abalone "closed season". Currently, a split closure to include one summer month is enforced for the commercial industry, and also for northern California sport divers. The effect of these measures has yet to be assessed. Minimum size limits exist for each species which conserve only the reproductive contribution by young and smaller adults.

THE DEVELOPMENT OF ABALONE MARICULTURE IN CALIFORNIA

It is a commonly held misconception that abalone culture in the United States was modeled after methods established in Japan. However, little technical information on critical aspects of larval and postlarval culture of abalone by Japanese biologists was available to the first entrants into the field in the 1960s. Consequently, the methods developed for culture of all stages of American abalones are quite different from those practiced in Japan (Leighton 1987). More recently, several attempts have been made in California to apply traditional Japanese hatchery methods, but generally the results of these approaches have not been encouraging (see Hatchery Methods, next section).

Pacific Mariculture (Pigeon Point, CA) began to explore possibilities for culture of abalone as seed for reintroduction to native habitat in 1964. Success was achieved in production of juvenile red abalone. Also, spawnings in tanks holding several species yielded hybrid combinations (Owen et al. 1971; Owen and Meyer 1972[3]; Leighton 1987). Experimental planting of juvenile abalone was done, but emigration and mortality at the local offshore site limited returns. At the time, the Department of Fish and Game could not grant exclusive fishery rights to in-sea mariculturists for "undersize native" abalones. Proprietary "nonnatives" (in this case, hybrids) did poorly in the Pigeon Point area. Accordingly, Pacific Mariculture redirected its attention to the production of oyster spat and abandoned further abalone mariculture efforts (B. Owen 1968[4]).

In 1967, California Marine Associates (H. Staton, D. Leighton, and J. Perkins) launched the first large-scale abalone mariculture program in North America with the goal to produce red abalone in land-based tank systems for direct sales to the seafood market. Thousands of seed were provided to the California Department of Fish and Game for their first attempts to plant abalone in the natural environment (Bjornson 1970; Bailey 1973). Commercial quantities of young adult red abalone were soon reared in large concrete raceway tanks. Following an instructive, but problematic, cooperative experimental program with the Atlantic-Richfield Company to conduct containment grow-out of abalone beneath an offshore oil production platform (Gealy and Lindstedt-Siva 1984[5]), California Marine Associates was reorganized to become Estero Bay Mariculture. In 1982, further reorganization occurred and a new company, The Abalone Farm, Inc., was formed. Refinements in the basic culture procedures and expansion of the hatchery and raceway systems have boosted production significantly. In 1986, over 180,000 small adult red abalone (5–10 cm) were marketed, valued at over $400,000 (F. Oakes 1987[6]).

[3]Owen, B., and R. Meyer. 1972. Laboratory hybridization in California abalones (*Haliotis*). Pacific Mariculture, Pigeon Road Point, Pescadero, CA (Unpubl. rep.)

[4]B. Owen, Pacific Mariculture, Pigeon Point Road, Pescadero, CA 94060, pers. commun. 1968.

[5]Gealy, F., and J. Linstedt-Siva. 1984. Containment culture of abalone beneath an offshore platform. Talk presented at Aquaculture Symposium, May 1984, Southern California Academy of Sciences, Los Angeles.

[6]F. Oakes, The Abalone Farm, Inc., P.O. Box 136, Cayucos, CA 93430, pers. commun. 1987.

Ab Lab (J. McMullen, proprietor) began operation in 1972 at Port Hueneme, CA. Initial efforts yielded seed size (2–4 cm) red abalone grown entirely within small tanks. A change to containment culture using mesh-ended polyethylene drums held beneath a dock at the harbor entrance has improved production of larger abalone (4–8 cm). A new market developed in specialty seafood restaurants and sushi bars in the Los Angeles area in the early 1980s. Ab Lab marketed approximately 150,000 young red abalone in 1986 (J. McMullen 1987[7]; Hamilton 1988).

Monterey Abalone Farms began research and development activities for culture of red abalone in 1972. Using an old building on Cannery Row in Pacific Grove, annual production gradually increased, but difficulties stemming in part from what was considered an inordinate volume of governmental restriction and consequent efforts in compliance (Armbrister 1980) prompted a move of the operation to Hawaii. There, an experimental program is underway to apply artificially upwelled seawater to the culture of cold-water mollusks in the tropics (Fassler 1987).

Institutional research efforts related to abalone mariculture have been diffuse. Studies have been based largely at the University of California at San Diego (Leighton 1968, 1972, 1974; Leighton and Lewis 1982) and Santa Barbara (Morse et al. 1977, 1979, 1984), the California Department of Fish and Game laboratory at Carmel (Ebert and Houk, 1984), and World Research, Inc., a San Diego nonprofit research organization (Leighton et al. 1981, Leighton 1985, 1987). Many findings from these studies have added to the fund of knowledge facilitating the development of abalone mariculture.

NORTH AMERICAN SPECIES OF IMPORTANCE TO MARICULTURE

Aside from a single rare and small species occurring in deep water off the Florida Keys (*Haliotis pourtalesii*), North American abalones are to be found only on the Pacific coast. There, seven species and two subspecies of haliotids occur (Fig. 2). In the order of their historical value to California fisheries (prior to 1975) are the red, *H. rufescens*; pink, *H. corrugata*; green, *H. fulgens*; white, *H. sorenseni*; and black, *H. cracherodii*. The remaining species are small and of minor commercial interest.

Descriptions and ranges for the northeastern Pacific abalones are to be found in the literature (McLean 1969; Haaker et al. 1986). An earlier account by Cox (1962) and a later one by Hooker and Morse (1985) contain inaccuracies which make those papers less useful. Generally, the red and black abalones are distributed most broadly, while the green, pink, and white abalones are found only south of the cold-warm transition near Point Conception, CA (Fig. 2.).

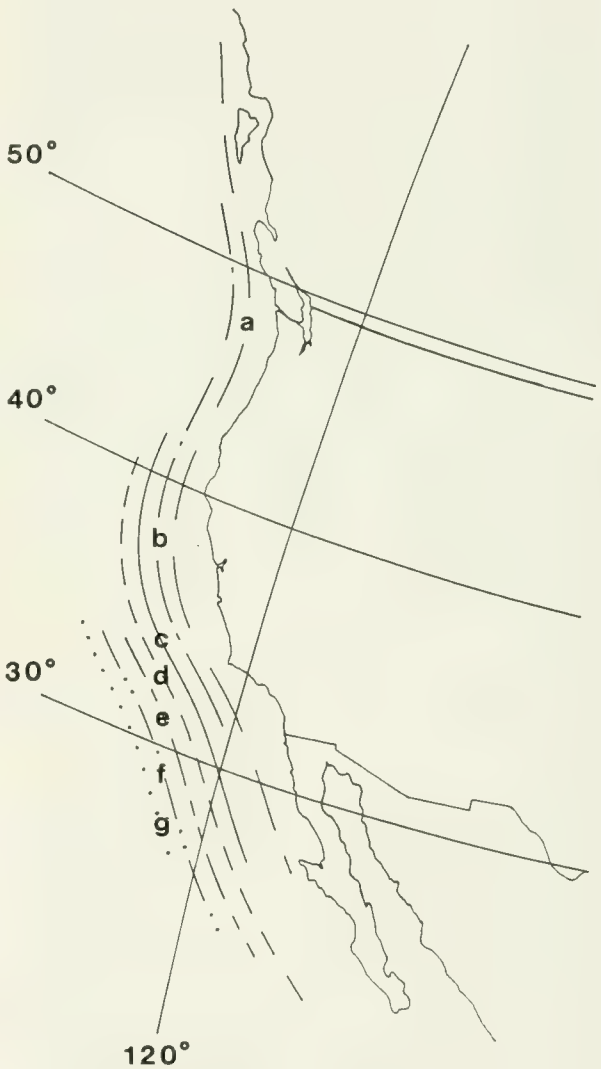

FIGURE 2.—Latitudinal distribution of abalones along the Pacific coast of North America. Range limits are as provided by Haaker et al. (1986). a. *Haliotis kamtschatkana* (two subspecies, *H. k. kamtschatkana* north of Monterey Bay, and *H. k. assimilis* south of that point). b. *H. walallensis*. c. *H. rufescens*. d. *H. cracherodii*. e. *H. fulgens*. f. *H. corrugata*. g. *H. sorenseni*.

[7]J. McMullen, Ab Lab, U.S. Navy Civil Engineering Laboratory, Port Jueneme, CA 93043, pers. commun. 1987.

All California species have now been cultured experimentally, but the red abalone remains as the principal species for mariculture. This cold-water abalone has been the focus of attention chiefly because it thrives along the central California coast where early mariculture operations were most effectively established. Furthermore, most biological information was available for the red abalone and the species was most attractive from the mariculture standpoint, being the largest member of the genus and having the strongest commercial history. It has proved, fortunately, to be the most easily cultured California abalone (Leighton 1987).

The green abalone has shown special potential for mariculture in systems utilizing thermal effluent (Leighton 1974, 1985; Leighton et al. 1981) and other means to provide temperatures in the range 20°–28°C (e.g., thermal enhancement in passive solar or geothermal systems). In the late 1970s, Leighton transported larval and juvenile green abalone to mariculture facilities in Hawaii and Florida, finding survival and growth to be exceptional in those tropical regions (Leighton 1987). The green abalone is especially attractive since its growth rate is significantly increased at higher water temperatures; young adults gain nearly 5 cm/yr in shell diameter (Leighton 1974, 1985; Leighton et al. 1981).

Pink and white abalones have been cultured on a small scale (Leighton 1972, 1974). The black abalone, a shallow-water species of lower commercial grade, is broadly tolerant of temperature in adult stages, but larvae from California races have thermal limits similar to that of the cold-water red abalone. Black abalone have been reared from laboratory-spawned eggs (Leighton 1974, unpubl. data). Flat, *H. walallensis*, and threaded, *H. kamtschatkana assimilis*, abalones have also been cultured in research projects in Southern California. The pinto abalone, *H. k. kamtschatkana*, is receiving attention as a mariculture subject in Washington and British Columbia (Fletcher 1987). All species of eastern North Pacific abalones have been found to hybridize in the laboratory with varying degrees of success. In most cases larvae and subsequent stages are fully viable and young adults fertile (Owen and Meyer 1972 [fn. 3]; Leighton and Lewis 1982). Some hybrids exhibit features which promise to be advantageous to mariculture, including environmental adaptability, improved growth rate and hardiness, and possibly refinements in quality of flesh (Leighton 1987).

AMERICAN ABALONE CULTURE TECHNOLOGY

As stated earlier, methods to culture abalone in California were developed quite independently from those practiced in Japan. Generally, the emphasis by U.S. culturists has been on production of crop animals of small adult size directly marketable in the domestic trade. Abalone are reared to sizes of 7–10 cm either within specialized tanks on shore or in containments held in protected ocean waters. In Japan, however, young abalone are usually released to the natural environment at a size of 2–5 cm for continued growth over periods of 2–4 years until a marketable size (7–10 cm) is reached (Saito 1984). Few attempts have been made in that country to rear abalone to adults under the controlled environmental conditions afforded by appropriate tank systems. However, highly elaborate concrete and plastic structures of many designs to provide protective substrate and improved foraging are now being applied to abalone grow-out in the sea (Sheehy and Vik 1981). Coupled with habitat improvement (i.e., algal afforestation and predator control), these in-sea approaches to increase abalone production are gaining success (see Alternatives for Grow-Out). The economic and other risks associated with such measures have constrained development by private enterprise in the United States.

Hatchery Methods

The requirement of North American species of abalones for rapidly moving, well-aerated seawater led to the early development of culture tanks which provided full circulation. Circular tanks proved most effective, and Leighton (1977) introduced such a tank in which rotary flow was easily maintained by air-lift with minimum energy input. Self-cleaning features accompany the vortical drive, airlift return design (Fig. 3). Originally devised for culture of relatively sessile marine invertebrates, the tank allows maximum control, a rapid circulation, and foam fractionation via the return line. These features are effective for culture of swimming larvae and early settled stages. Following use by us (California Marine Associates), new entrants adopted similar tank designs for postlarval and juvenile culture. Now typical of U.S. hatchery tank arrays, round tanks stand in marked contrast to the "raceways" and immersed plastic panels employed in Japan and elsewhere.

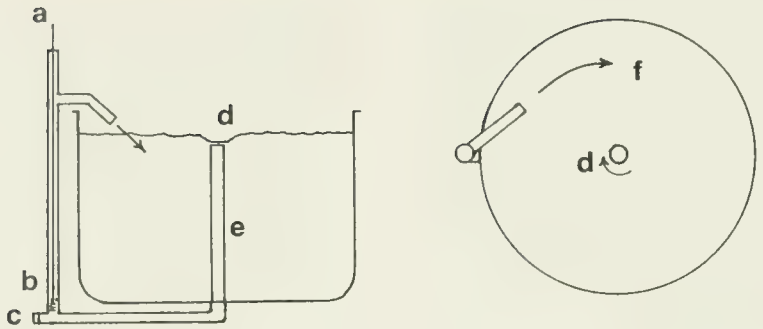

FIGURE 3.—Cylindrical larval and postlarval rearing tank. Vortical drive airlift circulated tank in its simplest form. Tank is self-cleaning and vertical extension for air-lift pipe allows foam fractionation (from Leighton 1965 (unpubl. data), 1977). a. Airline; b. air stone at base of airlift column; c. drain port, normally closed; d. vortex; e. central stand pipe, removable; f. return flow.

Gravid adult abalone may be induced to spawn using several different methods. Thermal shock, still used in some hatcheries in Japan (Ino 1980), was initially used in U.S. abalone culture, but soon abandoned in favor of the method of Kikuchi and Uki (1974) using UV-irradiated seawater. Also available is the hydrogen peroxide method developed by Morse and associates (Morse et al. 1977, 1978). Each approach has its advantages and disadvantages (Ebert and Houk 1984; Leighton and Lewis 1982). Usually broodstock are spawned in separate containers, then gametes are collected and combined to yield the highest fertilization rates. Eggs are subsequently washed and incubated under static conditions at temperatures most appropriate for the species (Leighton 1972, 1974).

Embryos generally hatch from eggs in 12–18 hours as trochophore larvae. Soon after hatching, larvae display a negative geotaxis (Leighton 1972, 1974), swimming at the surface in culture containers for 6–12 hours. This behavior, common to red, green, pink, and white abalones, has been mistakenly regarded as a positive phototaxis in observations with *H. rufescens* by some workers (c.f., Ebert and Houk 1984; Hooker and Morse 1985). Light, however, has a negligible influence on the swimming behavior of these species in the trochophore and pre-eyespot veliger larval stages. Larvae then become increasingly demersal with age. Culture routines, involving water changes and concentration of larvae, take advantage of these behavioral characteristics.

In the hatchery, larvae are generally reared through swimming stages (approximately one week) in culture containers of small volume (5–10 L) with careful attention to water quality, bacterial contaminants, temperature, and density. Highly filtered (ca. 1 μm) seawater, antibiotic treatment, and daily water changes promote maximum survival (virtually 100%) and normal development when larvae are incubated at densities of 2 individuals/mL or less (Leighton 1977). Some laboratories utilize mesh-bottom plastic cylinders immersed in a highly controlled, circulating system similar to that employed in bivalve culture (Ebert and Houk 1984).

The temperature dependency of early development for the principal California species is described by Leighton (1972, 1974). Cold-water species (red, pinto, flat, and white) have thermal optima for larval development in the range of 12°–16°C. The black abalone, while broadly tolerant of temperature in adult stages, is similar to the cold-water species in larval life (optimum 14°–18°C; Leighton 1987). The green abalone is distinctive, having a thermal optimum for larval development in the range of 18°–24°C (Leighton 1974, 1985; Leighton et al. 1981). The pink abalone is intermediate in its thermal requirements. In contradiction to a recent report by Hooker and Morse (1985), only the green abalone among California species may be considered "thermophilic". Hatcheries involved in culture of red, pink, and green abalones must observe the temperature requirements of these species closely.

Advanced larvae are induced to settle and begin metamorphosis using a variety of methods (see Problem Areas). Commonly, larvae at an age of about six days are admitted to small volume tanks supporting thin coatings of benthic microflora (chiefly diatoms and associated bacteria) wherein larvae settle within several hours

to two days. It was observed early in red abalone hatchery research that larvae introduced to tanks precolonized by crustose coralline red algae settled promptly. Tanks which had recently held healthy conspecific juveniles, the walls of which presented a well-grazed microfloral substrate, proved especially beneficial to successful settlement and metamorphosis (Leighton 1987). Several sources of "inducers" which effectively prompt settlement and metamorphosis appear to exist (see Problem Areas).

Settled larvae immediately begin feeding on bacteria and other microflora. Metamorphosis commences with loss of the velar cilia and larval operculum. Deposition of peristomial shell is evident within another day, but metamorphosis is a complex and gradual transition. The first respiratory pore is formed at the end of postlarval life (onset of the early juvenile stage), generally as the abalone reaches 1.5–2.5 mm (age about six weeks).

Postlarval attrition continues to remain as the principal "efficiency bottleneck" in abalone culture. Under usual hatchery conditions, survival and normal development for swimming larvae are close to 100% (Leighton 1977, 1985), but mortalities occur in a large percentage of metamorphosing postlarvae with the result that early juveniles represent at best 5–10% of the number of larvae at settling. Declines are most evident during the fourth to sixth week postfertilization. However, when conditions are optimized (usually in small volume containers), survival through postlarval life may be over 25% (c.f., Leighton et al. 1981; Table 1). Losses during critical early benthic stages may thus be reduced significantly by appropriate control and care to include frequent water changes, maintenance of clean conditions, and supplying microalgal foods on a regular basis (see Problem Areas).

Juvenile Culture

Once postlarval abalone begin to form the first respiratory pore, the pallial system (gills and associated structures) and other features of anatomy become more typical of the adult. The juvenile stage commences at this point and extends to young adulthood and onset of sexual maturity. Dietary changes occur in conjunction with development; first-settled metamorphosing postlarvae feed upon smaller microflora (diatoms, sessile flagellates, and bacteria). Early juveniles rely on many larger microalgae, but undergo a dietary transition to include a variety of green, red, and brown macroalgae as advanced juvenile stages are approached. The dietary transition to macroalgae occurs in many species at about 1 cm shell length (4–6 months), but is usually never complete as microalgal films may be ingested and metabolized through adult life (Leighton 1987).

When juvenile abalone reach about 3 mm, they are transferred to larger tanks precolonized by appropriate algae. Transfer is achieved with negligible losses by simple brushing (Leighton

TABLE 1.—Size increase for young adult red and green abalones provided two brown algal diets.

		Mean shell length gain (μm/d)					
		Haliotis rufescens period			*Haliotis fulgens* period		
Alga	Group	I	II	III	I	II	III
Macrocystis pyrifera	A	64.9	57.7	61.7	33.4	45.9	54.0
	B	35.8	71.0	65.9	31.4	17.8	36.8
$\bar{x}$	(S.D.)		59.5	(12.4)		36.6	(12.5)
Egregia menzesii	A	76.3	91.9	81.5	86.4	101.6	93.0
	B	60.5	97.3	78.8	71.4	90.0	66.0
$\bar{x}$	(S.D.)		81.1	(12.9)		84.7	(13.5)

Mean shell length increases (μm/d) for young adult abalone held in duplicate groups (6 individuals/group). Abalone were fed to satiation throughout three feeding periods of 40–50 days each. All abalone were in the size range 5–10 cm; groups were held in 10 L plastic pails receiving ambient seawater at 1 L/min and vigorous aeration. To promote continuous feeding, freshly collected algae were provided in excess (ca. 100 g) weekly. *Haliotis rufescens* observations were made in winter, 13°–17°C; *H. fulgens* in summer and fall, 18°–22°C.

1977, 1985). Some culturists employ chemical relaxants (such as Benzocaine at 100 ppm) to facilitate transfer, but associated losses may be high. The latter method becomes necessary when original culture tanks are large and immovable.

Japanese methods for abalone culture, outlined by several researchers (Kan-no 1975; Ino 1980; Grant 1981; Uki 1981), almost universally employ elongate rectangular "raceway" tanks holding vertically suspended corrugated plastic panels for culture of postlarvae and juveniles. Larvae are allowed to settle directly on the plastic substrates in special tanks prior to transfer to the raceways. Young abalone are reared to 1–2 cm under those conditions. While some hatcheries release the juveniles in the sea for fishery enhancement at that point, others retain the abalone in mesh-bottom drums held upright in larger tanks or supported by rafts in protected marine areas for growth to 3–5 cm (Kan-no 1975).

In the two principal hatcheries for red abalone in California (The Abalone Farm and Ab Lab), culture through early juvenile stages is achieved employing similar systems. However, these groups differ markedly in their approaches for rearing young abalone to market size (4–10 cm). The Abalone Farm practices raceway culture in which juveniles are reared in a series of concrete troughs through which seawater cascades from upper to lower members. Vigorous aeration is supplied intermittently and seawater flow rates vary from 0 to 200 L/min, depending on the pumping schedule. The kelp, *Macrocystis pyrifera*, is the principal food provided, although many species of red, green, and brown algae are available locally in large quantity and are supplied supplementally. Ab Lab transfers juvenile red abalone at about 1 cm to containment structures held in the channel at the entrance to Port Hueneme Harbor. Large polyethylene drums (ca. 55 gal capacity) with plastic or stainless steel mesh capped ends are secured in a horizontal position to braces in racks, all immersed to a depth of a few feet beneath a pier. Each drum receives several thousand individuals initially. *Macrocystis* forms the majority of the diet. Thinned with growth, the young abalone are reared to a size of 4–5 cm and sold live to specialty seafood dealers in the Los Angeles area (Hamilton 1988).

The relatively slow growth rate typical of abalones (ca. 2.5 cm/yr) has been limiting to commercial production by mariculture. However, some species exhibit accelerated development and growth at water temperatures higher than normally experienced in nature. The Pacific abalone has been reared in thermal effluent seawater from an electric power plant in Japan during the cold season (McBeth 1972). Growth rate of the California green abalone was almost doubled when reared at 24°–28°C in power plant effluent in an extensive 4-yr study (Leighton et al. 1981; Leighton 1985). Two new programs in abalone mariculture are being established to utilize thermal energy from coastal power facilities in Southern California for commercial production of this valuable species (see Future Prospects).

ALTERNATIVES FOR GROW-OUT

High costs of grow-out in most land-based systems make methods to rear abalone from juveniles to marketable adult stages in the sea attractive. As discussed earlier, emphasis in Japan has been placed on the design and testing of a diversity of artificial habitats for environmental improvement and partial containment for abalone in the ocean. In that country the largely government-supported hatcheries supply seed abalone to members of fishery cooperatives for planting on improved and controlled areas of sea bottom (Saito 1984; Sheehy and Vik 1981). The introduced abalone are allowed to mature for a period of 2–4 years before final harvest. Much attention has been given means for enhancing survival and growth of these crops by increasing production of kelps and other seaweeds as well as expanding the substrate necessary for concentrated "farming" of abalone. Yields of marketable abalone have been increased appreciably in some areas as these two approaches are coupled with measures to harvest or otherwise reduce numbers of predatory fish and invertebrates (Ino 1980; Uki 1981).

In the mid-1960s, significant advances were made in the United States toward kelp habitat improvement (North 1976). Areas of rocky bottom maintained in minimal algal productivity by large concentrations of sea urchins are often those with the highest potential for algal production and abalone recruitment. A valuable tool for restoration of ecological balance resulted from the finding by Leighton that calcium oxide effectively reduced numbers of overgrazing echinoids, fostering the return of *Macrocystis* and other vegetation with subsequent repopulation by diverse fauna (Leighton et al. 1966; Leighton 1971). Red and pink abalone populations returned to the Point Loma Shelf (San Diego) with

unusually heavy recruitment following treatment in 1963–65 of the area with quicklime to reduce sea urchin numbers (Leighton 1968). Interest is gaining in Japan to reclaim vast areas of potentially productive sea bottom limited by sea urchins (e.g., the "isoyake", or "pink rock", coralline algae/echinoid-dominated bottom) for increased abalone production using several approaches of physical habitat improvement, chemical treatment, and algal afforestation (Uki 1986[8]).

Several groups holding leases to areas of offshore California land are engaging in "sea-floor ranching" of abalone. In 1984, a total of about 50 acres had been leased for this purpose in southern California (Leighton 1984[9]). One individual (D. Gilbert, San Diego Mariculture) has liberated many millions of late-stage larvae onto rock bottom within boundaries of his lease holdings. Increases in population densities of seeded species are reported in preliminary surveys. Larval seedings often fail for a number of reasons, including "temporary settlement" (clinging while retaining the ability to swim once again; Leighton 1987), micropredation, and variable viability of different larval stocks. A successful field plant of larval *H. iris* in New Zealand has been reported (Tong et al. 1987). In that experiment, localized recruitment occurred, likely because larvae were released at an advanced age (13 days, Tong 1987[10]), thus reducing the opportunity for emigration.

It appears success of larval and juvenile plantings is dependent on a variety of factors (see Problem Areas). Extremely high losses of red abalone juveniles were reported soon after release off the California coast by Department of Fish and Game biologists (Tegner and Butler 1985). Introduction of young abalone to the marine environment is, however, quite unlike releasing trout fry in freshwater lakes and streams. Using "temporary protective habitats", Leighton (1985, 1987) found greatly improved survival of green abalone through reduced handling during transport and minimized predation during the critical 1–2 days following plants. This highly effective and low cost method uses shelters consisting of stacked corrugated PVC sheet (Fig. 4) which allow high density containment during transport and initial protection at the planting site, virtually eliminating "planting mortality". Survival one year after release, based on live recoveries, has been at least 20%; a highly conservative estimate since the planting areas were sampled without destructive approaches to open crevices or upturn large rocks (Leighton 1985, 1987). Likely a combination of controlled planting, habitat improvement, algal afforestation, and predator reduction will prove most effective for the success of seafloor ranching of abalone in California.

Experimental U.S. programs in containment culture carried out by private interests have included buoyed cages (Pacific Ocean Farms, Monterey), cylindrical modular habitats (Atlantic-Richfield Company/California Marine Associates, Santa Barbara), and bottom-secured concrete pipe sections. Containment culture in the sea presents advantages for concentration and protection not inherent in the more extensive approach of seafloor ranching. Under appropriate routines for feeding and maintenance, abalone may be reared at high densities, greatly simplifying the harvesting process. However, containment culture has, to date, proven expensive, not entirely free of predation problems (as young stages of crabs, seastars, etc. enter cages), and subject to destruction by heavy surge and entanglement by drifting kelp. Groups conducting studies in California have not solved all these problems. New designs of containment structures, which incorporate effective feeding systems, are simply monitored and are less susceptable to damage by physical forces are needed to advance technology in this area.

PROBLEM AREAS

The major technological impediments to full development of efficient abalone mariculture in North America appear to fall into three categories: 1) Yields of juveniles under hatchery conditions generally represent less than 10% of the larval stock; 2) conditions for optimization of the culture environment to promote maximum health and growth still require definition for each of the principal species cultivated; and 3) cost-effective methods and associated materials for grow-out, especially in the ocean, remain to be tested and applied on a commercial scale.

Abalone culture technology advanced rapidly

[8]N. Uki, National Research Institute of Aquaculture, Nansei, Mie 516–01, Japan, pers. commun. 1986.

[9]Leighton, D. L. 1984. Recent developments advancing aquaculture of abalone in southern California. Paper presented to Marine Aquaculture–Southern California, 1984 Symposium. Annual Meeting, Southern California Academy of Sciences, May 12, 1984, Los Angeles.

[10]L. Tong, Ministry of Aquaculture and Fisheries, Fisheries Research Center, P.O. Box 297, Wellington, New Zealand, pers. common. 1987.

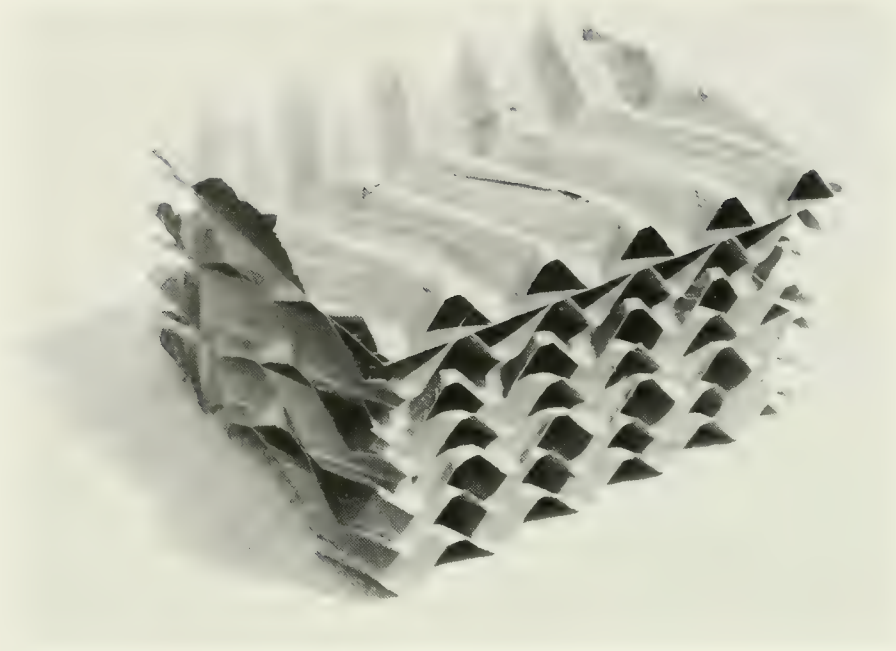

FIGURE 4.—Corrugated PVC sheet "temporary shelter" used to corral juvenile abalone in the hatchery, act as containment structure in transport, and serve as a stocking module and protective habitat for abalone planted in the marine environment. Over 200 juveniles (1–2 cm) may be contained in a single unit 20 × 20 × 30 cm. Abalone planted in these modules move to surrounding natural habitat within 24–48 hours without the high handling and predation mortality experienced with other methods (Leighton 1985). The layered plastic material is manufactured by B. F. Goodrich Company as "Bio-trickling Filter Medium" for use as a high surface to volume bacterial substrate applicable to sewage treatment processes. [Reference to trade name does not imply endorsement by the National Marine Fisheries Service, NOAA.]

in the private sector in the period 1970–75; highly effective methods were found to allow rearing of young red and green abalones through larval and early postlarval stages (ca. days 1–15) with minimal losses (Leighton 1987). These procedures have understandably been closely guarded by the pioneering U.S. abalone culturists. Recently, reports have appeared of new and grand technological advances in abalone culture through research in government (e.g., Ebert and Houk 1984) and academic laboratories (e.g., Hooker and Morse 1985). However, with the exception of the highly useful hydrogen peroxide method for induction of spawning in abalones (see Hatchery Methods), these studies have not, to date, added significantly to the technology for culture of larvae, postlarvae, and juveniles developed by the industry. Certainly, however, the research has contributed valuably to our understanding of basic biological processes (see below).

Interest has focused recently on the facilitation of settlement and prompting of metamorphosis by the addition of bioactive chemicals such as the neurotransmitter, gamma-aminobutyric acid (GABA) and related compounds (Morse et al. 1979). GABA does indeed cause a change in swimming behavior, possibly by affecting the bioelectric potential of cell membranes associated with the velar cilia (Koshtoyants 1960; Baloun and Morse 1984), with active settlement in mature and "competent" larval abalone. Behavior of larvae exposed to GABA, however, differs from that of larvae in the presence of "natural" inducers (see below). Exposure of larvae to GABA at concentrations in excess of 10^{-5} M is in fact lethal (Akashige et al. 1981; Slattery 1987), perhaps a consequence of excessive activation and/or blocking of receptor and transduction sites involving other vital functions. The role of GABA as a neurotransmitter is now well recognized in vertebrate and invertebrate systems. However, induction of settling and onset of metamorphosis in abalone larvae may be more complex than initially proposed (see Trapido-Rosenthal and Morse

1986) and may involve yet unidentified mediators and environmental cues. Further insight regarding use of GABA and other bioactive substances to prompt settlement and metamorphosis may be gained from the analysis and discussion by Pawlik (1988).

The behavior of larvae at settlement is critical to subsequent survival. In the presence of many elements common to the native environment of abalone, including microfloral colonies (diatoms, bacterial films, etc.), biliprotein-containing crustose red algae and cyanobacteria (Morse et al. 1984) and even "mucous trails" of conspecific juveniles (Seki and Kan-no 1981; Leighton 1985; Slattery 1987), advanced larvae of *H. rufescens* and other species examined exhibit a typical swimming behavior consisting of a series of landings and takeoffs as if testing the substrate prior to settlement. Surface acceptance is independent of orientation; settlement may be on container sides, bottom, or even on the undersides of included substrates. In contrast, in the presence of GABA, larvae often settle promptly (usually within 2 hours at 10^{-6} M), but almost exclusively on container bottoms. In the hatchery setting, the tank bottom rapidly becomes a hostile environment and larvae settled there soon succumb to bacterial overgrowth. Using diatom films and other natural substrates, dispersal is optimized and subsequent settling and metamorphosis are normal (Leighton 1977, 1985). GABA is not used routinely in commercial facilities for the reasons cited above.

In California abalone hatcheries, larvae at competence are admitted to tanks appropriately prepared for settling and metamorphosis containing partially cleared diatom coatings (Leighton 1977), other microflora, or traces of mucus and associated substances left by former conspecific occupants (Leighton 1985, 1987; Slattery 1987). In the early stages of red abalone mariculture (Leighton, pers. obs. 1970–75) crustose coralline red algae (*Lithothamnion* and related forms) were cultured within special postlarval culture tanks. Settlement on coralline surfaces was often intense, and subsequent survival and growth of postlarvae was excellent. However, juveniles larger than 5 mm derived decreased nutriment from the coralline-benthic diatom substrate, necessitating their transfer to tanks precolonized by diverse microflora and to which macroalgae were supplied as foods. This observation is in confirmation of results (Leighton 1968: table XXX) showing reduced nutritional benefit of crustose coralline algal substrates for juvenile *H. rufescens*. It was also found in early hatchery operations that larval settling and postlarval success were greatly improved in fiberglass tanks which had recently held conspecific juveniles and adults (Leighton, pers. obs. 1971). More recently, Japanese biologists have found a similar benefit for larval recruitment to exist in *H. discus hannai* (Seki and Kan-no 1981).

As noted earlier, postlarval attrition still limits the efficiency of abalone mariculture, although claims to the contrary appear in the literature (e.g., Hooker and Morse 1985). Losses of 60–80% of postlarvae are commonly experienced during the second to sixth weeks following fertilization (Leighton 1985). While microbial pathogens have not often been demonstrated, a portion of the postlarval attrition may be due to disease. Mortalities may be reduced by providing intensive care to small-scale cultures for which antibiotic prophylaxis or other procedures are followed to minimize epizootic complications. A parasitic protozoan found especially lethal to juveniles younger than 190 days, but not injurious to more mature abalone, was isolated from an abalone hatchery in British Columbia (Bower 1987). Since many potentially deleterious organisms (e.g., *Vibrio* spp.) appear to thrive in decomposing organic matter, the well-managed hatchery is not likely to experience epidemic outbreaks of bacterial and protozoan diseases.

Regardless of the approach, a major portion of the postmetamorphic young eventually succumb before passing early juvenile stages (Leighton 1985). In practice, the high fecundity typical of mature female abalone acts in compensation for the large losses, and spawnings of small numbers of broodstock supply commonly several million larvae on each occasion.

The U.S. species of abalones most produced by mariculture, the red and the green, differ markedly in their requirements of nutrition as well as temperature (Leighton 1987). Kelps commonly used as foods for abalone in California mariculture are *Macrocystis pyrifera* and *Egregia menzesii*. The former is a valuable food for young red abalone, but a relatively poor diet for green abalone (Table 1). *Egregia* is effectively utilized by both species and is the diet of choice for culture of green abalone (Leighton et al. 1981). *Laminaria farlowii*, common in southern California, is also a productive diet, especially for green abalone. Mixed algal diets yield superior growth (Leighton 1968, 1977).

In hatchery systems, holding abalone at high stocking densities and providing satiation feeding, optimization of flow and exchange rates, pH, oxygenation, and other factors is essential for best animal health and growth. Often all requirements appear not to be met in tank rearing systems, however. Growth rate and vitality are generally greatly improved when abalone are matured in the sea in appropriate containments (see Alternatives for Grow-Out).

Growth of the industry in Southern California has been limited by land availability, water quality, and regulatory constraints. Central and northern California offer a far greater extent and variety of coastal sites, but temperature optimization, food availability, salinity reduction, and, at some locations, pollution add to operational limitations. Aside from certain locations within Puget Sound, WA and contiguous areas of Canada, most coastal regions in the Pacific Northwest present similar problems. Failure of some recent mariculture ventures has been due, in part, to inattention to some of these considerations.

FUTURE PROSPECTS

Successes in production and marketing by the existing abalone mariculture concerns in California are stimulating interest among new groups. At least three additional groups are planning shore-based abalone culture operations in the state at this time: Pacific Mariculture, Inc., Santa Cruz (P. Scrivani 1988[11]); Abalone Resources, Inc., Guadalupe; and Marine Bioculture, Inc., Carlsbad. Most will concentrate on production of small adult red abalone. Marine Bioculture will produce green, pink, and red abalones. Total annual production from expanded activities at the Abalone Farm, the Ab Lab, and the newer organizations could reach 100 t by 1995 and 250 t by the year 2000. Harvests from seafloor ranching of red abalone may increase rapidly and match the onshore production by that time. Thenceforth, yields from expanded in-sea programs (both containment culture and seafloor ranching) are expected to gain appreciably as the pertinent technology and cost/benefit factors are improved, and as seed stock becomes more universally available from the land-based hatcheries.

[11]P. Scrivani, Pacific Mariculture, Inc., 100 Shaffer Rd., Santa Cruz, CA 95060. PMI is distinct from PM, Pigeon Point, CA.

The potential for effective abalone mariculture both onshore and in the sea off Baja California, Mexico, is exceptional. To date mariculture of red, pink, green, and black abalones has been largely experimental in that country, but it is expected commercial operations will develop there soon (Aguirre 1987).

A forecast of significant growth in the abalone production industry over the next decade applies to the entire North American Pacific coast from Baja California to Alaska. The frontier now lies in the sea with a promising evolution of effective approaches to both managed cultivation by seafloor ranching and concentrated production within containing structures.

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A Key to Genera of the Penaeid Larvae and Early Postlarvae of the Indo-west Pacific Region, with Descriptions of the Larval Development of *Atypopenaeus formosus* Dall and *Metapenaeopsis palmensis* Haswell (Decapoda: Penaeoidea: Penaeidae) Reared in the Laboratory

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ABSTRACT: The penaeid prawns *Atypopenaeus formosus* Dall and *Metapenaeopsis palmensis* Haswell were induced to spawn and their larvae and postlarvae were cultured in the laboratory. Three protozoea, three mysis, and early postlarval substages are described for each species. A key to genera of the penaeid larvae and early postlarvae of the Indo-west Pacific region was constructed from this information, from other unpublished data from our own larval reference collection, and from previously published larval descriptions. The key, based entirely on laboratory-reared larvae, identifies the genera *Atypopenaeus, Macropetasma, Metapenaeopsis, Metapenaeus, Parapenaeopsis, Parapenaeus, Penaeus,* and *Trachypenaeus*. A sternal spine formula, a previously undescribed taxonomic character, is used for identifying postlarvae.

Twelve genera of penaeid prawns are found in the Indo-west Pacific: *Atypopenaeus*, *Funchalia*, *Heteropenaeus*, *Macropetasma*, *Metapenaeopsis*, *Metapenaeus*, *Parapenaeopsis*, *Parapenaeus*, *Penaeopsis*, *Penaeus*, *Trachypenaeopsis*, and *Trachypenaeus*. Most of these genera are widespread and common; the exceptions are the monospecific genus *Macropetasma*, which occurs only near the southern coast of South Africa, and *Heteropenaeus* and *Trachypenaeopsis*, which are widespread but rare (Dall el al. in press).

In spite of the worldwide distribution, abundance, and commercial importance of penaeids, ecological studies of their larvae have been hampered by taxonomic problems (Rothlisberg et al. 1983a). Several keys to larval penaeid genera have been published; however, none of these are suitable for use in the Indo-west Pacific region. Cook's (1966a) key to the Gulf of Mexico penaeid genera was a milestone, and remains the most useful reference. However, many Indo-west Pacific genera do not occur in both regions (e.g., *Atypopenaeus* and *Metapenaeus*) and therefore could not be included. *Xiphopenaeus* is included but does not occur in the Indo-west Pacific. *Sicyonia* and *Solenocera*, which Cook included, are now regarded as separate families in the superfamily Penaeoidea (Bowman and Abele 1982).

The keys of Hassan (1974), Haq and Hassan (1975), and Muthu et al. (1978) dealt with three genera in the Indo-west Pacific—*Penaeus*, *Metapenaeus*, and *Parapenaeopsis*—while Paulinose (1982) covered all genera except *Heteropenaeus* and *Macropetasma*. He also included the nonpenaeids *Sicyonia*, *Aristaeomorpha*, and *Solenocera*. However, many of the identifications in Paulinose's work are based on doubtful reconstructions from the plankton and the key has several practical shortcomings (see Discussion).

Penaeus and *Metapenaeus* have worldwide commercial importance in fisheries and aquaculture, and the larvae of many species have been reared in the laboratory and described (for review see Dall et al. in press). There have been very few laboratory studies that describe the larval morphology of the remaining penaeid genera in the Indo-west Pacific region. *Parapenaeopsis stylifera* larvae were reared and described by Rao (1973) and Hassan (1984). Thomas et al. (1975) also reared the larvae in the laboratory but provided no figures or detailed descriptions. *Macropetasma africanum* was reared and described by Cockcroft (1985). Heldt (1938) described *Parapenaeus longirostris*, but all

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stages after protozoea I are based on exuviae of a single surviving specimen. *Trachypenaeus* larvae were described by Kirkegaard (1969), but only the protozoea I were reared in the laboratory; later stages were isolated from preserved plankton catches. The only other description of *Trachypenaeus* is by Pearson (1939), who also used a combination of plankton-caught and laboratory-reared larvae. The present study is the first description of larvae of any species of either *Atypopenaeus* or *Metapenaeopsis*, based on laboratory-reared specimens.

To date, our published studies of larval prawns in the Gulf of Carpentaria have dealt exclusively with the genus *Penaeus* (Rothlisberg et al. 1983a, 1985, 1987; Rothlisberg and Jackson 1987). The characteristics of this genus are well established and their larvae are quite distinct from those of other genera (Cook 1966a). In order to study other genera, we have reared larvae of all six penaeid genera which are found in the Gulf of Carpentaria: *Metapenaeus*, *Metapenaeopsis*, *Penaeus*, *Atypopenaeus*, *Trachypenaeus*, and *Parapenaeopsis*. For all but one genus we now have a reference collection of protozoea I through to postlarvae; for *Parapenaeopsis* we have only the nauplius and protozoeal stages (Rothlisberg et al. 1985).

In assembling this key to genera of Indo-west Pacific penaeid larvae, we have used both our own reference material and information from previously published descriptions and keys. We have relied completely on existing descriptions for *Macropetasma* (Cockcroft 1985) and *Parapenaeus* (Heldt 1938; Pearson 1939; Paulinose 1979), genera not represented in the Gulf of Carpentaria and hence absent from our reference collection. Several workers who have described larvae from plankton samples claim to be able to identify the genus or even the species of the larvae. In the absence of supporting evidence from laboratory-reared larvae we have not used these descriptions in constructing our key. No reliable information about *Funchalia*, *Heteropenaeus*, *Penaeopsis*, and *Trachypenaeopsis* is available as they have never been reared in the laboratory.

MATERIALS AND METHODS

Gravid female *Metapenaeopsis palmensis* selected from trawl catches near Groote Eylandt in the western Gulf of Carpentaria in November 1983 and from off Cairns, northeast Queensland, in April 1985 were brought to the Cleveland laboratory. Gravid female *Atypopenaeus formosus* were collected from commercial trawl grounds in Moreton Bay, adjacent to the Cleveland laboratory, in January 1985.

When female prawns arrived at the laboratory, one eyestalk was ablated and the prawns were placed in a 90 L fiberglass aquarium with 4 cm of clean sand substrate. Seawater in the aquarium was continually replaced at approximately 1 L per minute, and any eggs or larvae were retained by a 90 μm mesh screen on the overflow. Prawns were fed daily on a frozen mixture of prawn and squid. The aquarium water was inspected each morning for eggs. When eggs were detected they were examined microscopically and, if embryonic development was normal, the female prawns were removed and preserved. When the eggs hatched, the nauplii were siphoned off, their abundance was estimated, and they were transferred into culture vessels at a density of approximately 100 nauplii per liter.

The culture vessels used were round-bottomed, 100 mm diameter Pyrex[1] tubes of 3 L capacity, with aeration supplied through a nipple molded into the bottom of the tube. The tubes were placed in environmental cabinets that enabled control of temperature (27°C) and of photoperiod (12 h:12 h light:dark). On alternate days, approximately 2.5 L of water were drawn off from the larval cultures through a 140 μm screen, and replaced with 1 μm filtered seawater.

For larval food, the marine alga *Tetraselmis suecica* was produced by batch culture in 20 L glass carboys. During the log growth phase, 13 L of algal culture were removed and the algal cells concentrated using a modified cream separator. The aerated concentrate was stored at 4°C and used as stock for feeding the larvae. The stock was replaced every 3–4 days.

Twice daily, beginning at late nauplius stage and continuing through to postlarva, sufficient algal concentrate was added to the larval cultures to maintain an algal cell density of approximately 1.5×10^5 cells per mL. Cell density in the larval cultures was estimated by fluorometry based on the relationship between fluorescence and cell density (P. C. Rothlisberg[2]). After the larvae reached mysis I, freshly hatched, heat-

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[2]Rothlisberg, P.C., Division of Fisheries, CSIRO Marine Laboratories P.O. Box 120, Cleveland, QLD 4163, Australia, unpubl. data.

killed *Artemia* nauplii were added daily, to a final concentration of 2–5 nauplii per mL.

Larval samples were removed from the cultures twice daily and preserved in 2% formaldehyde. At this sampling frequency, at least two samples were taken from any substage. For microscopic examination the preserved larvae were cleared in a polyvinyl alcohol solution to which Chlorazol Black had been added (Perkins 1956), and permanent slides both of whole animals and of dissections were made in this medium. For each larval substage described, at least five individuals were examined except where fewer larvae in good condition were available (Tables 1, 2). Where possible, the larvae examined came from different spawnings; otherwise, they came from the same spawning but were taken at different times.

Figures were drawn with the aid of a camera lucida used on a Wild M20 compound microscope. Measurements were made with a calibrated ocular micrometer. Body length was measured from the anterior border of the carapace (excluding the rostrum) to the posterior border of the telson, excluding any spines, and carapace length was measured to the posterior border of the carapace, along the midline.

RESULTS

General development

Atypopenaeus formosus and *Metapenaeopsis palmensis* followed the normal development pattern for penaeid larvae (Dall et al. in press): a number of nauplius substages, three protozoea substages, three mysis substages, and a series of postlarva substages gradually leading toward the juvenile form. While it may be possible to identify unknown penaeid nauplii into groups of one or more genera, preliminary studies confirmed the findings of Cook (1966a) that reliable generic identification of nauplii is not possible. To increase the numbers of cultured larvae available for sampling in later substages, the nauplius substages were not sampled and therefore are not described.

The protozoea I of both species was characterized by separate cephalothorax and abdomen, undeveloped eyes (which may be visible beneath the carapace), and a lack of uropods. Protozoea II had stalked eyes and a rostrum, while protozoea III had spines on a variable number of the abdominal segments and separate uropods. Mysis I lacked abdominal pleopods, mysis II had pleopods of a single segment, while the abdominal pleopods in mysis III had two segments. During the postlarval substages the pleopods became setose and the pereopod exopods became reduced. We have not attempted to describe specific instars or molt numbers of the postlarvae. Instead we have presented a single description which is representative of the first few instars; it is based on larvae sampled within two to three days of the first appearance of postlarvae. Earlier or later instars will, of course, differ in some respects. The most obvious changes with age are that the length of the 2nd antennal flagellum increases, the dorsal rostral spines increase in number, the telson becomes more pointed, the number of telson spines decreases, and the number of telson setae may increase.

Atypopenaeus formosus

The details of setation and segmentation for the various appendages are given in Figures 1 to 7 and in Table 1. Only general features, and those with some taxonomic significance, are described in the text below. For each major stage, the important features that do not vary between substages are presented first, followed by a brief description of the characteristics of each substage.

PROTOZOEA. Second antenna 0.7–1.0 times length of 1st in each substage. Setal formula of 2nd antennal protopod and endopod 1+2+2 [hereafter referred to as the 2nd antennal formula: the numbers of setae at the distal end of the protopod (Fig. $1d_1$), partway along the 1st endopod segment (Fig. $1d_2$), and at the distal end of the 1st endopod segment]. Second antennal exopod (Fig. $1d_3$) with 9 or 10 setae along inner margin, including those on distal segment. Telson with 7+7 setae in each protozoeal substage.

Protozoea I (Table 1, Fig. 1a) with pear-shaped carapace, less than half of total length, bearing a pair of frontal organs without overlying spines. Long labral spine present (Fig. 1b). Mandible asymmetry not yet pronounced, each mandible having a single, freestanding tooth between incisor and molar processes (Fig. 1e). First maxilla (Fig. 1f) protopod with 2 lobes, epipod (Fig. $1f_1$) with 4 long setae; 2nd maxilla protopod with 5 lobes (Fig. 1g). Segmentation of 1st and 2nd maxillipeds indistinct and variable (most common arrangement

TABLE 1.—Summary of larval characteristics of *Atypopenaeus formosus*. BL = body length (mm), number to left of colon indicates number of segments and numbers to right are setal counts for each served on different individuals. "*" indicates more than 10 setae too densely clustered to count appendage. Setal numbers are totals of all setal types on any segment. Reference to figures will

	Protozoea I (Fig. 1)	Protozoea II (Fig. 2)	Protozoea III (Fig. 3)	Mysis I (Fig. 4)
Number examined	8	8	10	8
BL mean (range)	0.7 (0.6–0.9)	0.9 (0.8–1.2)	1.6 (1.4–1.7)	2.0 (1.8–2.1)
CL mean (range)	0.3 (0.2–0.4)	0.4 (0.4–0.5)	0.6 (0.5–0.6)	0.6 (0.6–0.8)
First antenna				
Proximal part	3:1,2,5	3:1,6,5	4:0–2,1–3,3,5	3:6–7,4,3–5
Outer ramus	—	—	—	1:3
Inner ramus	—	—	—	1:1
Second antenna				
Protopod	2:0,1	2:0,1	2:0,1	2:0,0
Blade (seg: inner,outer)	9:9–10,2	9:9–10,2	10–12:9–10,2	1:8–11,1
Flagellum	2:4,4	2:4,4–5	2:4,4–5	1:4
Mandible				
Movable teeth (a:b)[1]	1:1	1:5	2:6	3:7
Palp	—	—	—	—
First maxilla				
Protopod	1:4–6/4	1:5–6/5–6	1:4–6/7–9	1:5–7/8–10
Endopod	3:2,1,4–5	3:2,1,4–5	3:2,1,5	3:1–2,0–1,4–5
Epipod	1:4	1:4	1:4	1:4
Second maxilla				
Protopod	1:6–7/1–2/3/ 3–5/2	1:8–10/2–3/2–4/ 4–7/2–3	1:9–10/3–4/4/ 4–5/2–3	1:12–14/4–6/5–10/ 7–8/3
Endopod	4:3,2,1–2,3	4:2,1–2,2,3	4:2–3,2,2,3	4:2,1–2,2–3,2–3
Epipod	1:4	1:5	1:5	1:7
First maxilliped				
Protopod	1–2:1–2,5–8	2:4–6,6–9	2:5–8,9–12	2:6–8,10–15
Endopod	4:3,1–2,2,5	5:3,2–3,2–3,2,4–5	4:3,2,1–2,5	4:2,2,1–2,3–4
Exopod	1:7	1:7	1:9	1:10
Second maxilliped				
Protopod	2:1,3	2:0–2,3	2:3,4–7	2:2–3,5–7
Endopod	4:1,1,1,5	4:1–2,1,1–2,5	4:2–3,1,2,4–6	4:4,3,1–2,3–4
Exopod	1:5–6	1:6	1:6–7	1:7
Third maxilliped				
Protopod	—	1:0	1:0	2:0,2–5
Endopod	—	1:0	1:3–4	5:1–2,2,1–2,3,4–5
Exopod	—	1:2–3	1:3–6	1:5–9
First percopod				
Protopod	—	—	—	2:0,0
Endopod	—	—	—	1:5–7
Exopod	—	—	—	1:11–15

[1]"a" side fewer teeth, "b" side more teeth. No attempt was made to match mandibles to either left or right sides.

CL = carapace length (mm). For each entry, unless otherwise indicated, segment from proximal to distal. "–" indicates range of setal numbers obreliably. Numbers separated by "/" are setal counts for separate lobes of an show distribution of setae along segments.

	Mysis II (Fig. 5)	Mysis III (Fig. 6)	Postlarva (Fig. 7)
Number examined	6	4	5
BL mean (range)	2.0 (1.8–2.1)	2.3 (2.2–2.4)	2.2 (1.9–2.7)
CL mean (range)	0.6 (0.6–0.7)	0.7 (0.6–0.8)	0.7 (0.6–0.8)
First antenna			
Proximal part	3:10–13,3–6,4–8	3:5–13,3,4–6	3:10–16,5–9,1
Outer ramus	1:4	2:0,4	3:0,0,3–5
Inner ramus	1:2–3	1:0	3:0,2–6,3–4
Second antenna			
Protopod	2:0,0	2:0,0	2:0,0
Blade (seg: inner,outer)	1:10–16,0	1:15–17,0	1:21–25,0
Flagellum	2:0,0–1	3:0,0,0	4:0,3,2,2
Mandible			
Movable teeth (a:b)[1]	2:7	3:6	0–1:1–5
Palp	—	1:0	2:2–5,5–15
First maxilla			
Protopod	1:6–7/8–14	1:6–7/10	1:7/10
Endopod	3:1–2,1–2,3–5	3:2,1,3–4	3:1,2,4
Epipod	0–1:4	—	—
Second maxilla			
Protopod	1:*/*/*/*/*	1:*/*/*/*/*	1:*/*/*/*/*
Endopod	4:2,1–2,2–3,2–3	4:2,1,0–1,3	1:*
Epipod	1:10–15	1:10–15	1:*
First maxilliped			
Protopod	2:6–8,8–12	2:5–8,13–15	1:*/*
Endopod	4:4,1–4,1–4,4	4:3,1–2,1–2,4–5	4:2,2,0,4
Exopod	1:6–7	1:5–7	1:5
Second maxilliped			
Protopod	2:2–3,5–7	2:3,4–5	2:4,*
Endopod	4–5:3,4,0–3, 3,4–5	5–6:3–4,3,0,2–3, 1–3,3–5	5:1,4–6,1,3,5
Exopod	1:3–5	1:4	1:5
Third maxilliped			
Protopod	2:0,2	2:0,1	2:1,3
Endopod	4:2,1,1,6	5:1,1–2,2–3,0,5	5:3,4,4,1,5–7
Exopod	1:3–6	1:4–7	1:6
First percopod			
Protopod	2:0,1	2:0,0	2:3,4
Endopod	2:2,3	4:0,1,2,4–7	4:1,3,5,3
Exopod	1:6–8	1:6–8	1:6

TABLE 2.—Summary of larval setation and segmentation of *Metapenaeopsis palmensis*. BL = body indicated, number to left of colon indicates number of segments and numbers to right are setal counts observed on different individuals. "*" indicates more than 10 setae too densely clustered to count appendage. "t" indicates terminal segment. Setal numbers are totals of all setal types on any seg-

	Protozoea I (Fig. 8)	Protozoea II (Fig. 9)	Protozoea III (Fig. 10)	Mysis I (Fig. 11)
Number examined	10	4	6	8
BL mean (range)	0.8 (0.7–0.8)	1.4 (1.4–1.5)	2.0 (1.9–2.1)	2.3 (2.1–2.7)
CL mean (range)	0.4 (0.3–0.4)	0.5 (0.5–0.6)	0.7 (0.6–0.7)	0.7 (0.6–0.8)
First antenna				
Proximal part	3:0–1,2,5	3:0–1,1–3,4–6	4:1,1,3,4–5	3:10–12,4,4–6
Outer ramus	—	—	—	1:4–5
Inner ramus	—	—	—	1:1–2
Second antenna				
Protopod	2:0,1	2:0,1	2:0,1	2:0,0
Blade (seg: inner,outer)	9:9–11,2	8–9:9–11,2	8–10:9–11,1	1:10–11,1
Flagellum	2:4,5	2:4,5	2:4,5	1:4
Mandible				
Movable teeth (a:b)[1]	1:2	1:4	2:6	3:7
Palp	—	—	—	—
First maxilla				
Protopod	1:5–7/3–5	1:6/6–7	1:4–8/8–10	1:6–8/8–12
Endopod	3:2–3,2–3,4–5	3:2,2,4–5	3:2,1–2,3–5	3:2,1–2,4
Exopod	1:4	1:4	1:4	1:4
Second maxilla				
Protopod	1:5–7/3/3/2–4/2	1:6–8/2/3–4/2/3–5	1:8–10/2–4/3–6/3–6/2–4	1:*/3–5/3–5/4–6
Endopod	4:1–2,1–2,2–3,3–4	3:1–2/1–2/2–3	4:2–3,2,2–3,2–3	4:2,1–3,1–3,3–4
Exopod	1:4	1:5	1:5	1:12
First maxilliped				
Protopod	1–2:12–17	2:5–9,8–9	2:5–11,8–10	2:8,11–13
Endopod	4:3–4,1–2,1,5–6	4:3,1–2,1–2,5	4:2–3,1–2,1–2,5	3–4:3,1–3,1,3–4
Exopod	1:7	1:7	1:8–10	1:10–11
Second maxilliped				
Protopod	1–2:5–7	2:4,3	2:3–4,5–7	2:4,7–8
Endopod	4:1–2,1–2,1–2,5	3–4:2,1,1,4–5	4:3,1–2,1–3,4–5	4:4,2,3–4,5
Exopod	1:6	1:6	1:8–9	1:5
Third maxilliped				
Protopod	—	1:0	2:0,0	2:0,4–5
Endopod	—	1:0	1:3	4–5:2,2–3,2–3,2,4–5
Exopod	—	1:2–3	1:4–5	1:5
First pereopod				
Protopod	—	—	—	2:0,2
Endopod	—	—	—	3:2,2,7
Exopod	—	—	—	1:7

[1]"a" side had fewer teeth, "b" side had more teeth. No attempt was made to match mandibles to either left or right

length (mm), CL = carapace length (mm). For each entry, unless otherwise for each segment from proximal to distal. "–" indicates range of setal numbers reliably. Numbers separated by "/" are setal counts for separate lobes of an ment. Reference to figures will show distribution of setae along segments.

	Mysis II (Fig. 12)	Mysis III (Fig. 13)	Postlarva (Fig. 14)
Number examined	5	4	3
BL mean (range)	2.7 (2.5–2.8)	2.8 (2.7–2.9)	2.8 (2.6–3.0)
CL mean (range)	0.7 (0.7–0.8)	0.8 (0.7–0.8)	0.7 (0.7–0.8)
First antenna			
Proximal part	3:6–10,8–12,4–6	3:12–16,5,5	2:17–25,8–12
Outer ramus	1:4–6	1:5	2:0,4
Inner ramus	1:1–2	1:3	1:2
Second antenna			
Protopod	2:0,0	2:0,0	2:0,0
Blade (seg: inner,outer)	1:15–18,0	1:16–21,0	1:25–28,2
Flagellum	4–5:0,0,0,0,2	5–9:3t	15–25:(all 0–1),6t
Mandible			
Movable teeth (a:b)[1]	3:7	3:7	0–3:0–6
Palp	—	1:0	2:5–9,12–20
First maxilla			
Protopod	1:4–8/8–10	1:6–8/8–11	1:4–8/9–13
Endopod	3:2,2,3	3:2,1–2,3–5	1:0–7
Exopod	—	—	—
Second maxilla			
Protopod	1:*/5/6–8/2–4/1–2	1:*/2–4/5–7/4–5/2	1:3–5/3–5/4–8
Endopod	3:2–4,2–4,3	3–4:(all 1–3)	1:4
Exopod	1:11	1:10	1:25–35
First maxilliped			
Protopod	2:8–9,10–16	2:5–9,13–16	1:20–25/10–15
Endopod	4:3–4,2–3,1,4	3–4:3,2,1,5	3:2,0,1
Exopod	1:7–10	1:8–10	1:5
Second maxilliped			
Protopod	2:3–4,8–10	2:3–5,8–10	2:1,7
Endopod	5:4,2–3,2,1–2,6	5:4,3–5,2–3,2–3,4–6	5:2–4,5,0,3,4–6
Exopod	1:6	1:5	1:0
Third maxilliped			
Protopod	2:0,2–3	2:0,1–2	2:1,0
Endopod	5:1–2,1–2,1–4,3,5	5:1–2,2–3,2–3,2,4	6:(all 3–6), 6t
Exopod	1:4	1:4–6	1:0
First pereopod			
Protopod	2:0,2	2:0,1–2	2:2,3
Endopod	4:1,1–2,2,3–4	4:0–1,1–2,2–3,4	4:2,0,2,6
Exopod	1:4	1:7–8	1:0

sides.

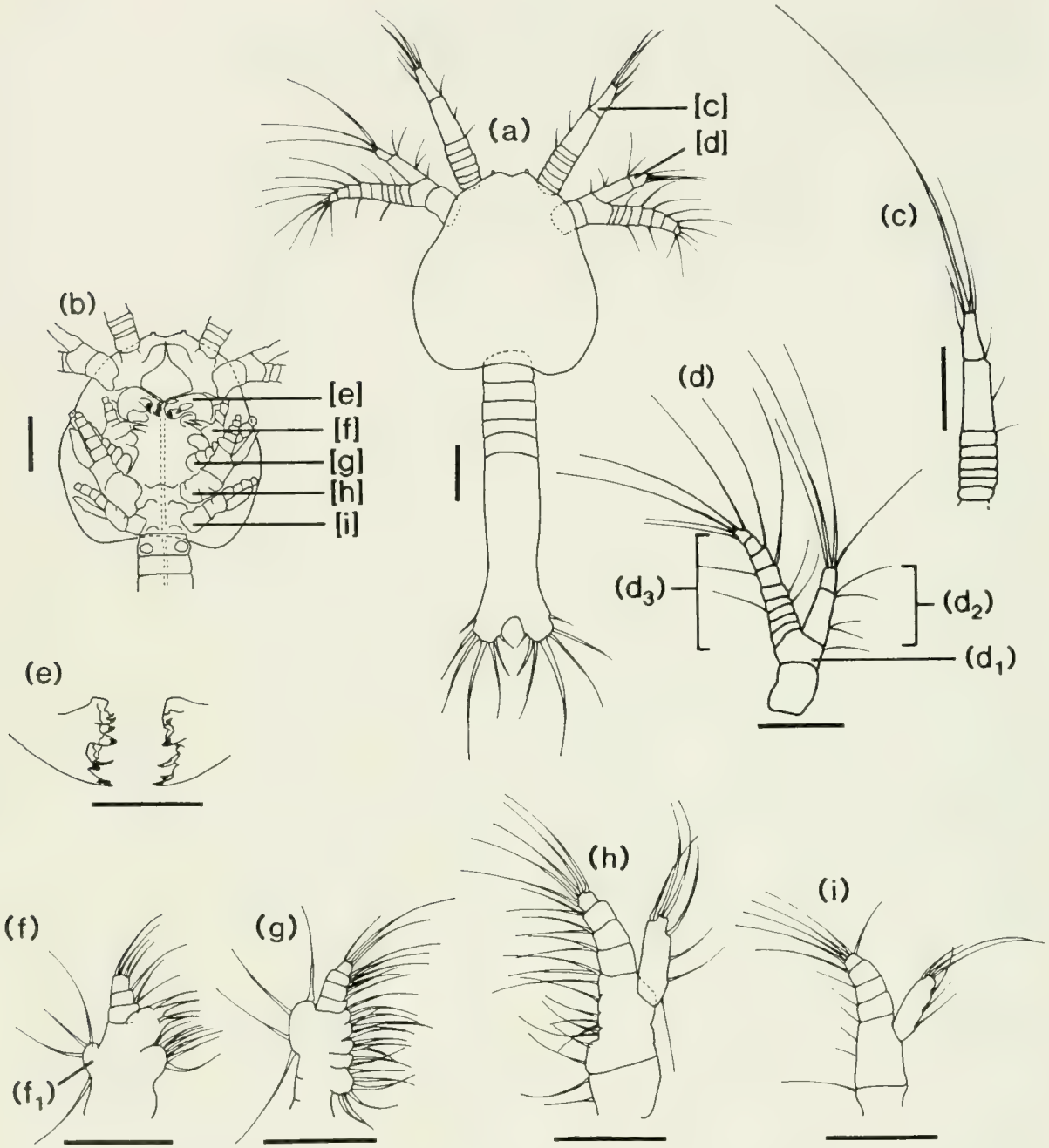

FIGURE 1.—*Atypopenaeus formosus* protozoea I. (a) whole animal, (b) ventral view of cephalothorax, (c) 1st antenna, (d) 2nd antenna, (d_1) protopod, (d_2) endopod, (d_3) exopod, (e) mandibles, (f) 1st maxilla, (f_1) epipod, (g) 2nd maxilla, (h) 1st maxilliped, (i) 2nd maxilliped. Letters in square brackets show origins of dissected appendages. Scale = 0.1 mm.

shown: Fig. 1h, i). Third maxilliped only a bud (Fig. 1b).

Protozoea II (Table 1, Fig. 2a) with long rostrum, extending beyond eye, and a single pair of supraorbital spines. Second antennal formula still 1+2+2 but first seta very small, sometimes difficult to see (Fig. 2c). Mandibles (Fig. 2d) now asymmetrical, one side with 5 serrate, free-standing teeth, other side only 1 (no attempt was made in any dissection to determine whether a particular mandible was originally from the left or the right side). First and 2nd maxillae (Fig. 2e, f), 1st and 2nd maxillipeds (Fig. 2g, h) similar to previous substage. Third maxilliped slightly more developed, biramous, however, still very small (Fig. 2i).

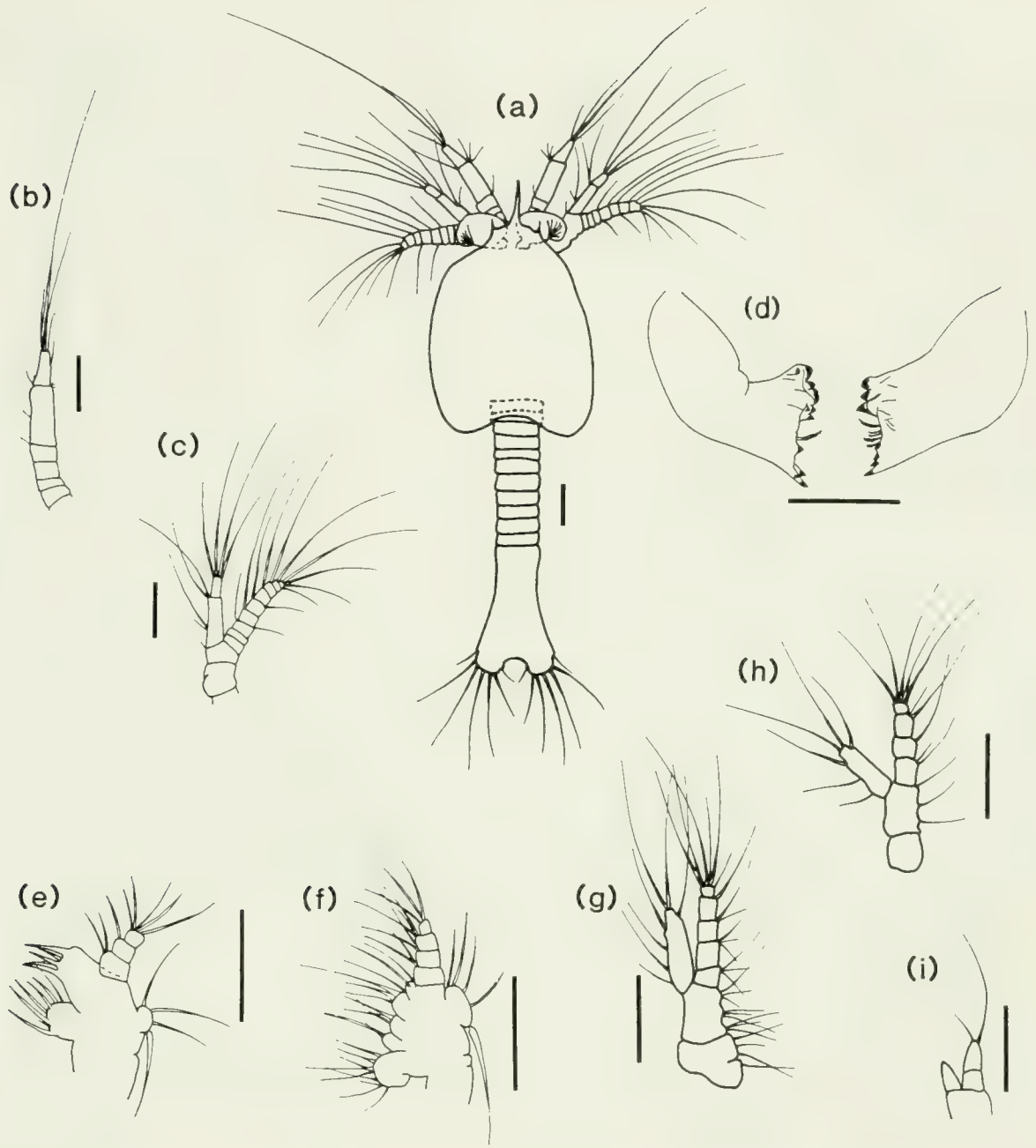

FIGURE 2.—*Atypopenaeus formosus* protozoea II. (a) whole animal, (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped. Scale = 0.1 mm.

Protozoea III (Table 1, Fig. 3a) retaining long rostrum and supraorbital spines. Some setae in 2nd antennal formula of 1+2+2 are small but always present (Fig. 3c). Maxillae (Fig. 3e, f), maxillipeds (Fig. 3g, h, i) similar to previous substage, although generally more robust and more setose. Dorsal spines occasionally on 4th abdominal segment and always on 5th; lateral spines on 5th and 6th segments (Fig. 3a). Uropods present (Fig. 3a).

MYSIS. Characteristics that are invariant in the mysis stage of *A. formosus* are rostrum extending beyond eye, lack of supraorbital and hepatic spines, presence of pterygostomial spine, 7+7 telson spines, 6th abdominal segment always

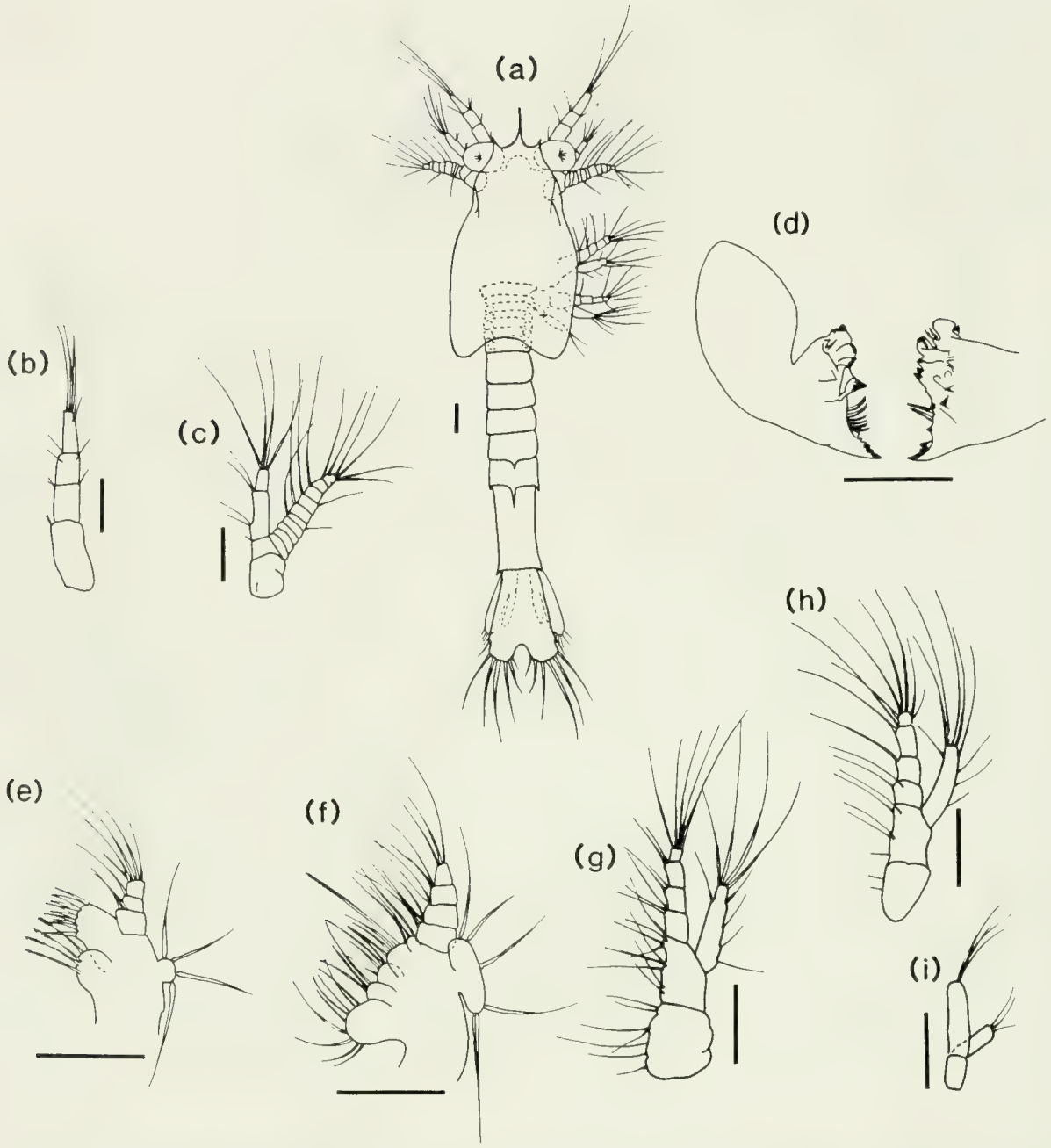

FIGURE 3.—*Atypopenaeus formosus* protozoea III. (a) whole animal, (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped. Scale = 0.1 mm.

bearing a dorsal spine, lack of lateral abdominal spines.

Mysis I (Table 1, Fig. 4) without rostral teeth. First antenna biramous, bearing a strong ventral spine on first segment (Fig. 4c). Second antenna devoid of segmentation on both endopod and exopod (Fig. 4d). Mandibles similar to those of protozoea III, although stronger and with more teeth (Fig. 4e). Structure of 1st maxilla (Fig. 4f) similar, but epipod on 2nd maxilla, the formative scaphognathite, is beginning to increase in size (Fig. 4g). First 2 maxillipeds similar to previous substage but 3rd much more elongate (Fig. 4h, i, j). Rudiments of chelae appearing on 1st 3 pereopods (Fig. 4k). Usually a small dorsal spine on 5th abdominal segment,

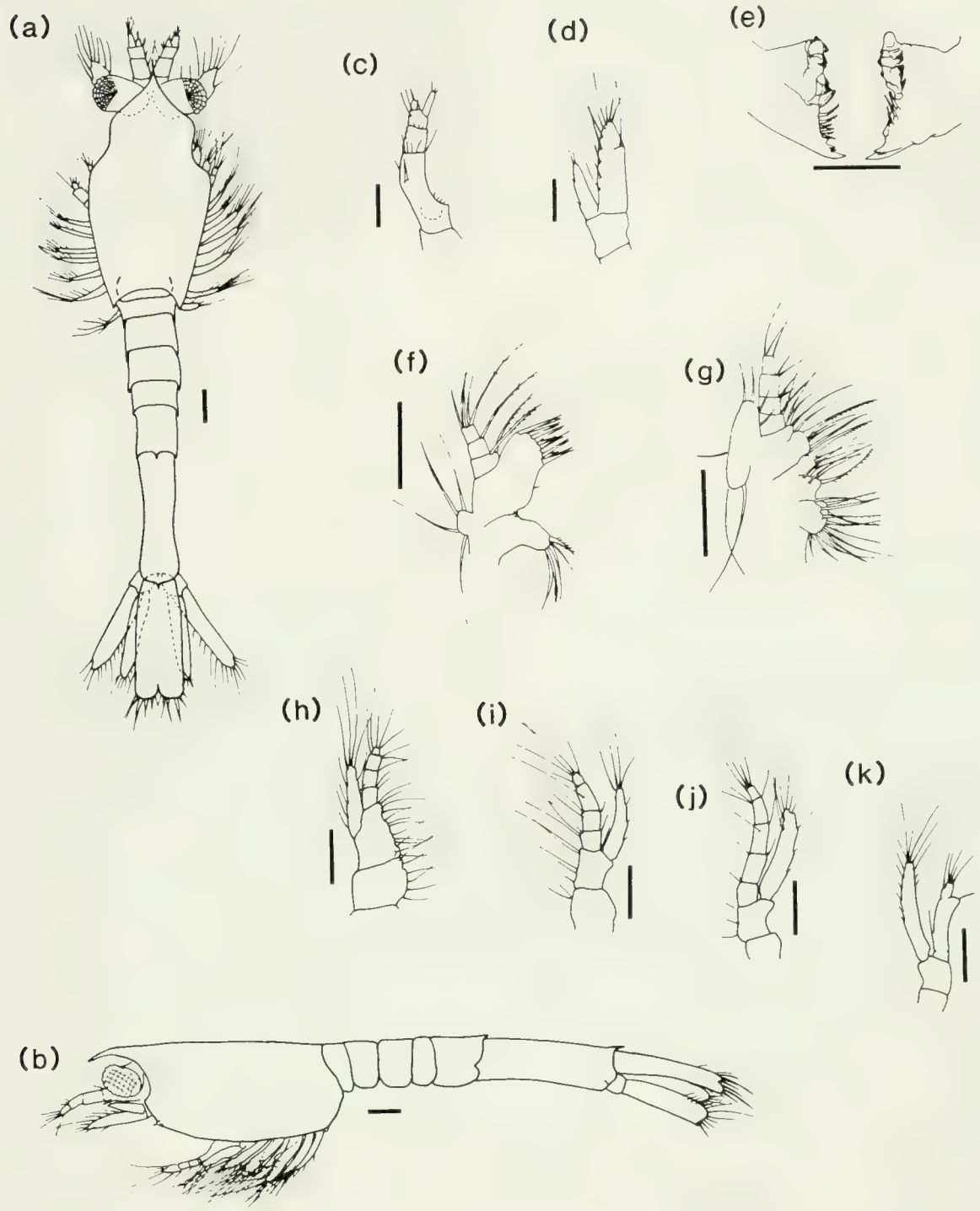

FIGURE 4.—*Atypopenaeus formosus* mysis I. (a) whole animal (dorsal view), (b) whole animal (lateral view), (c) 1st antenna, (d) 2nd antenna, (e) mandibles, (f) 1st maxilla, (g) 2nd maxilla, (h) 1st maxilliped, (i) 2nd maxilliped, (j) 3rd maxilliped, (k) 1st pereopod. Scale = 0.1 mm

and a large one on the 6th. Telson retaining deep cleft with 7+7 spines (Fig. 4a).

Mysis II (Fig. 5) still with no rostral teeth. Dorsal spine on 5th abdominal segment either missing or very small; spine on 6th segment remains. Small statocyst sometimes present in 1st antenna (Fig. 5b). Second antenna with spine on blade, flagellum of 2 segments about half as long as blade (Fig. 5c). First maxilla now without epipod, although a small protuberance sometimes remains (Fig. 5e). Epipod of 2nd maxilla further enlarged, more setose (Fig. 5f). First maxilliped stouter than previous, exopod much reduced in size (Fig. 5g). Second and 3rd maxillipeds changing little (Fig. 5h, i); chelae on pereopods clearly defined (Fig. 5j).

Mysis III (Fig. 6) with 2 dorsal rostral teeth. Only 6th abdominal segment with dorsal spine.

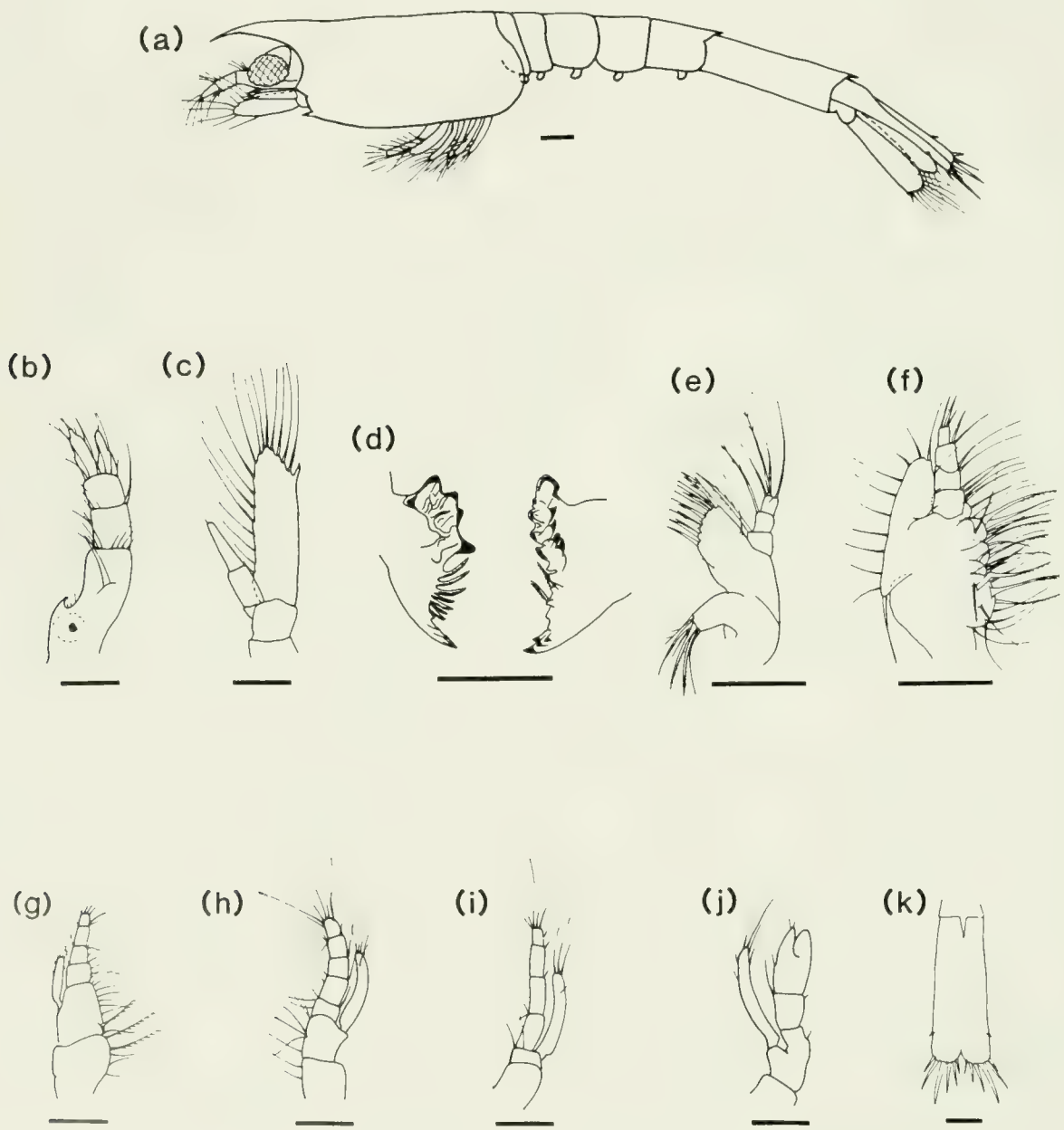

FIGURE 5.—*Atypopenaeus formosus* mysis II. (a) whole animal (lateral view), (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped, (j) 1st pereopod, (k) telson. Scale = 0.1 mm.

Statocyst now normally present (Fig. 6b), antennal flagellum about the same length as in previous substage (Fig. 6c). Mandible with unsegmented palp (Fig. 6d). First maxilla similar to previous substage (Fig. 6e); epipod of 2nd maxilla continues to become larger and more setose (Fig. 6f). Three maxillipeds now bearing rudimentary gills (Fig. 6g, h, i), which vary in size in different individuals; pereopods now have functional chelae (Fig. 6j). Shallow telson cleft remains (Fig. 6k).

POSTLARVA. The postlarva of *A. formosus* (Fig. 7) has a rostrum with 3 dorsal teeth and an epigastric tooth. Pterygostomial spine present, but no supraorbital or hepatic spine. Proximal

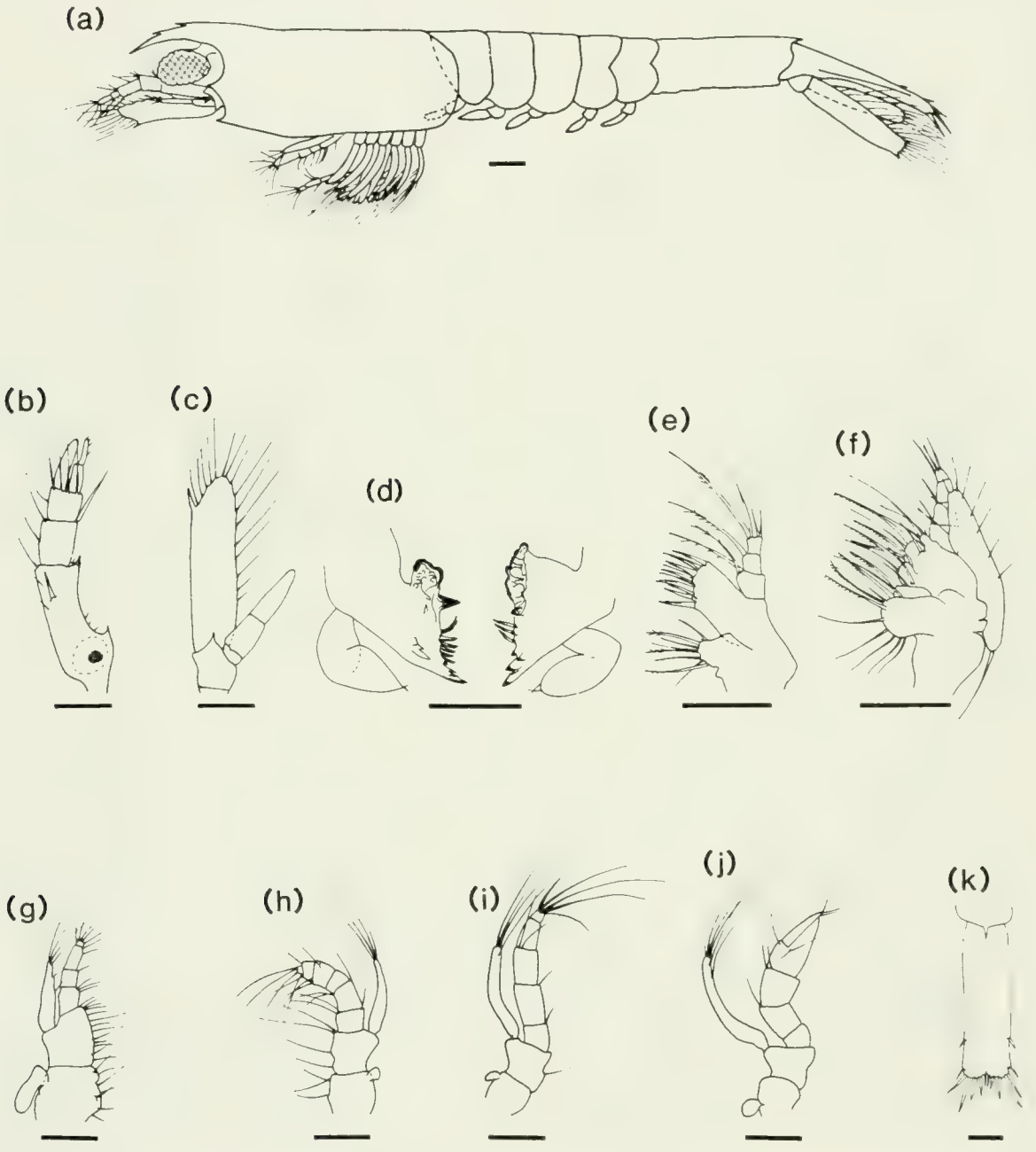

FIGURE 6.—*Atypopenaeus formosus* mysis III. (a) whole animal (lateral view), (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped, (j) 1st pereopod, (k) telson. Scale = 0.1 mm.

segment of 1st antenna with 1 spine near statocyst, 1 distally; 2 rami now elongated (Fig. 7b). Antennal flagellum almost as long as blade (Fig. 7c). Most fine teeth and grinding teeth absent from mandible, now bearing 2-segmented, setose palp (Fig. 7d). First maxilla (Fig. 7e) unchanged; epipod of 2nd maxilla (Fig. 7f) extends from base to tip. Exopod and endopod of 1st maxilliped reduced in size (Fig. 7g). Second maxilliped little changed (Fig. 7h), endopod of 3rd maxilliped long and slender (Fig. 7i). Pereopods and chelae longer and stronger (Fig. 7j). One long median sternal spine on 4th thoracic segment, and 1 short median sternal spine on 5th (sternal spine formula 0+0+0+1+1) (see Figure 15e). Only 6th abdominal segment with dorsal spine (Fig. 7a). Posterior margin of telson rounded, without cleft. Telson spine formula remaining 7+7 with additional 2 long, feathery submedian setae (Fig. 7k).

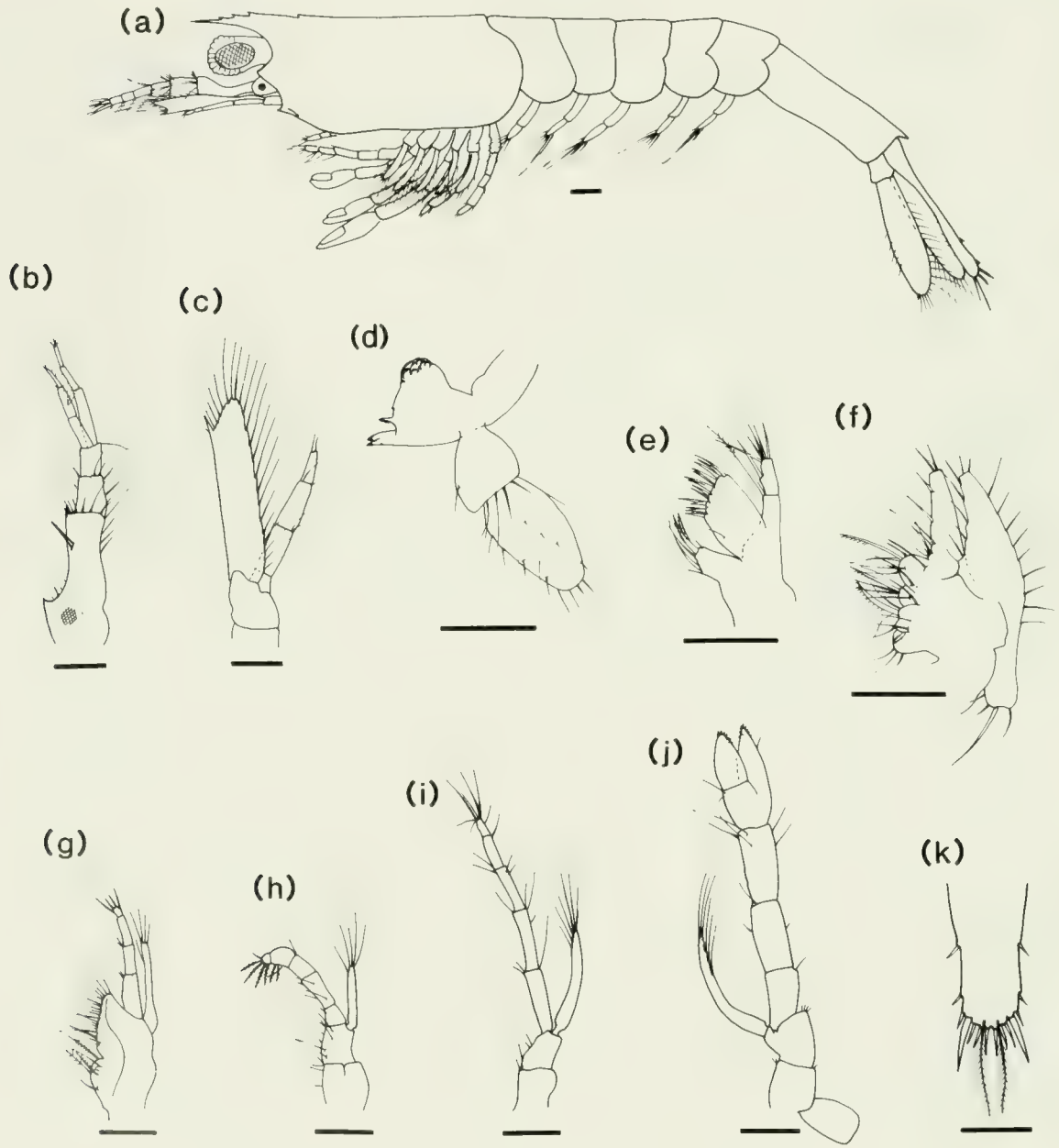

FIGURE 7.—*Atypopenaeus formosus* postlarva. (a) whole animal (lateral view), (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped, (j) 1st pereopod, (k) telson. Scale = 0.1 mm.

Metapenaeopsis palmensis

The details of setation and segmentation for the various appendages are given in Figures 8 to 14 and in Table 2. The general development of *M. palmensis* parallels *A. formosus*, and only significant differences are given in the following text.

PROTOZOEA. Second antenna 0.7–1.0 times length of 1st antenna throughout protozoeal stage; 2nd antennal formula 1+2+2. Telson setal formula of 7+7 does not change until mysis II. Exopod of 2nd antenna bears 10 or 11 setae along its inner margin.

First substage (Table 2, Fig. 8a) with oval carapace bearing frontal organs and, above them, a prominent pair of pointed spines projecting forward between the 1st antennae. Length of these spines approximately equal to

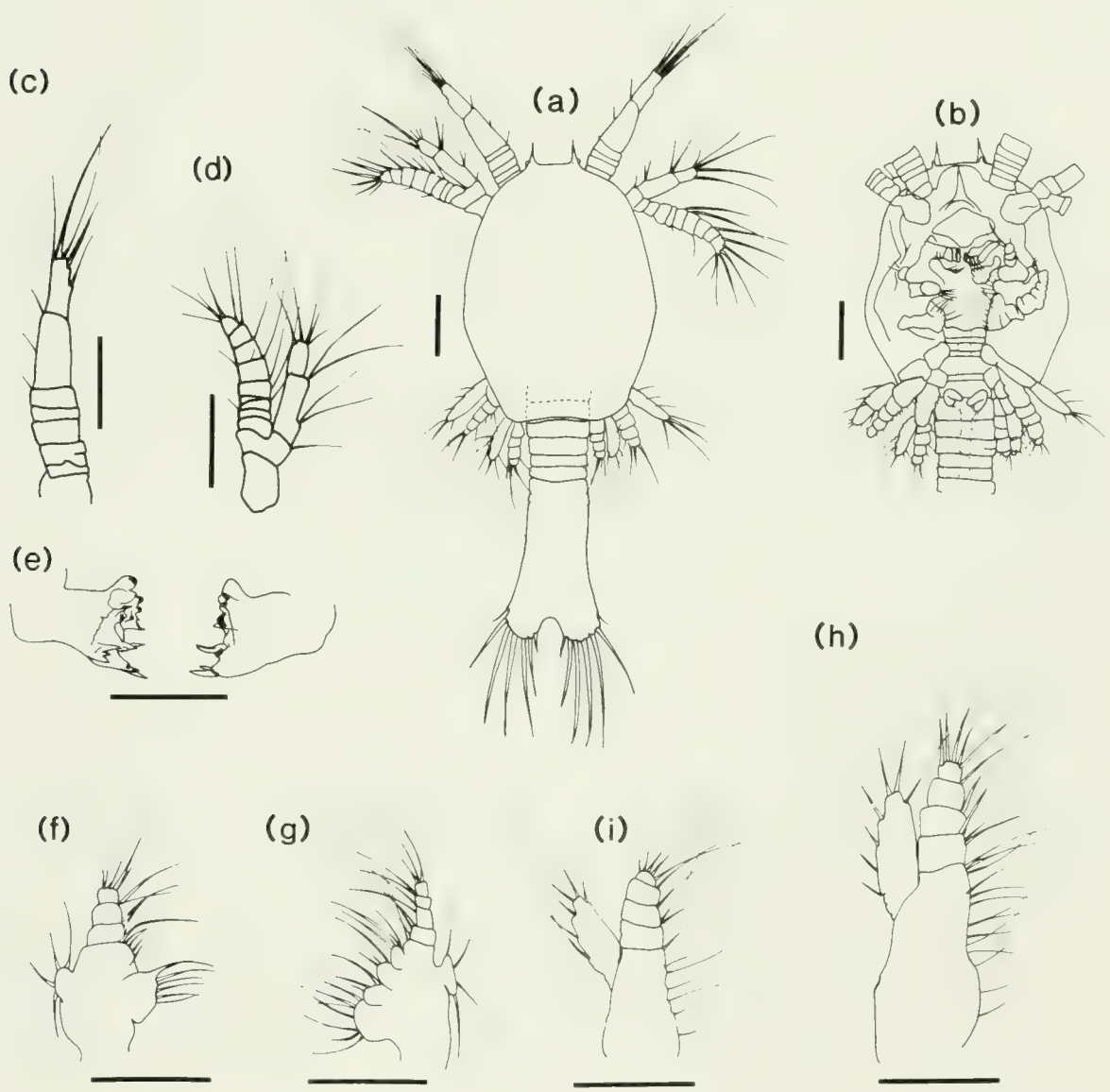

FIGURE 8.—*Metapenaeopsis palmensis* protozoea I. (a) whole animal, (b) ventral view of cephalothorax, (c) 1st antenna, (d) 2nd antenna, (e) mandibles, (f) 1st maxilla, (g) 2nd maxilla, (h) 1st maxilliped, (i) 2nd maxilliped. Scale = 0.1 mm.

diameter of basal segment of 1st antenna. Carapace length about half total length. Long labral spine (Fig. 8b). As in *A. formosus*, segmentation of 1st and 2nd maxillipeds variable and often indistinct (Fig. 8h, i). Second substage (Fig. 9) with long, down-curved rostrum extending beyond tip of eye. Two pairs of supraorbital spines. Both 1st and 2nd antennae stouter than *A. formosus* (Fig. 9b, c). In 3rd substage (Fig. 10) the inner supraorbital spines have almost disappeared, leaving only a protrusion in the carapace border or sometimes 1 or 2 small denticles (Fig. $10a_1$). Outer supraorbital spines remain distinct. Dorsal spines present on first 5 abdominal segments; lateral spines on 5th and 6th segments (Fig. 10a).

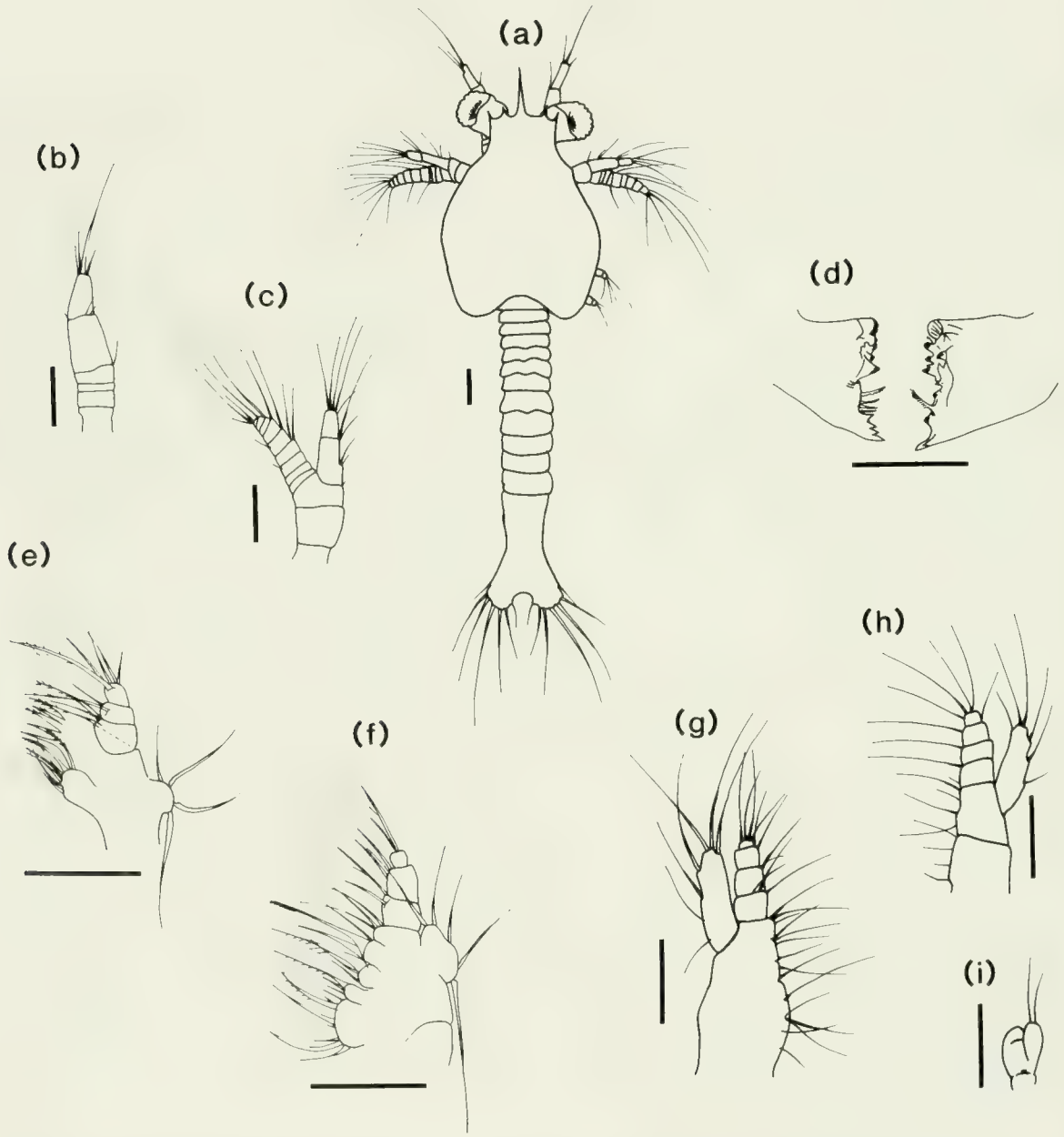

FIGURE 9.—*Metapenaeopsis palmensis* protozoea II. (a) whole animal, (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped. Scale = 0.1 mm.

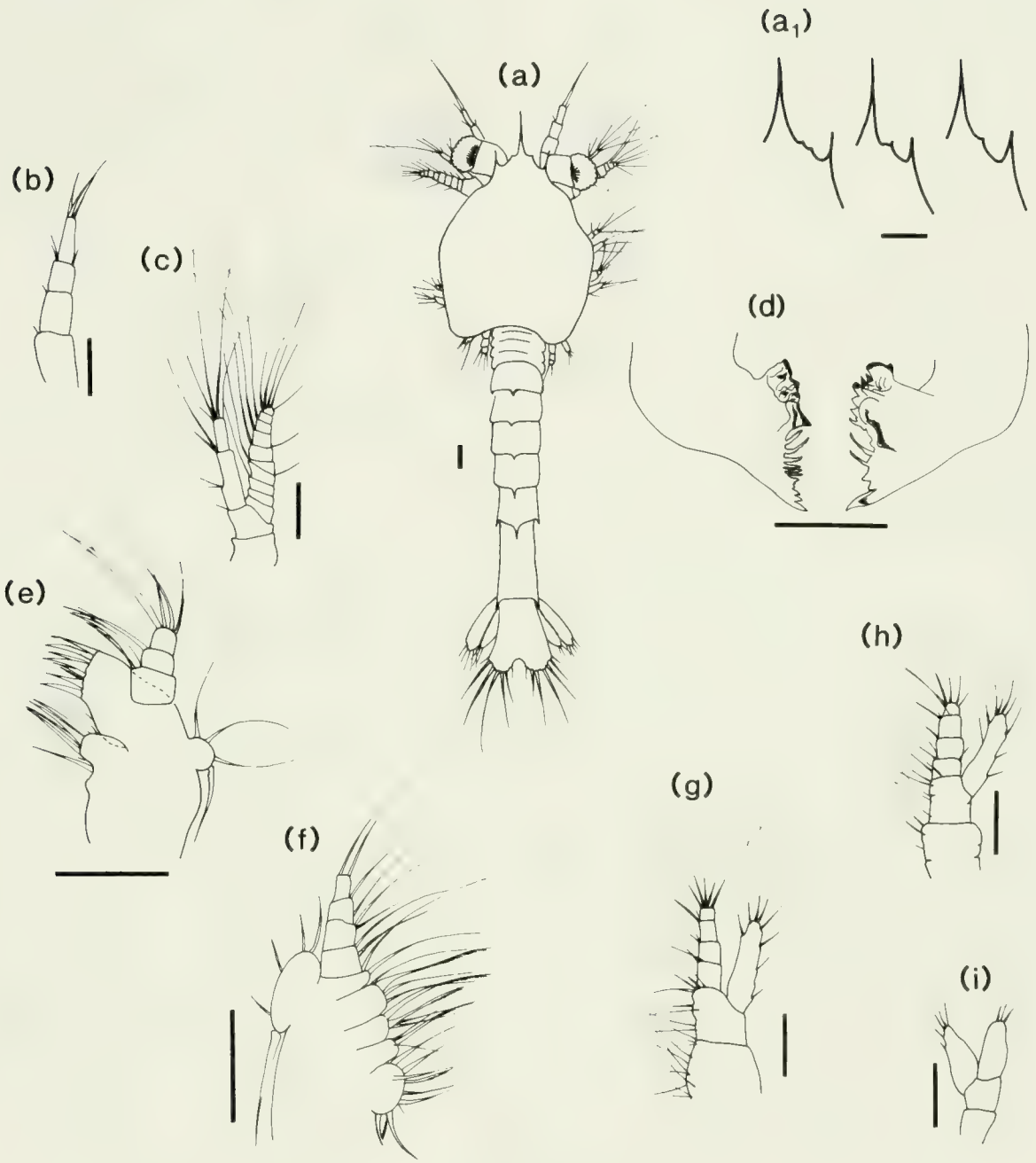

FIGURE 10.—*Metapenaeopsis palmensis* protozoea III. (a) whole animal, (a_1) detail – variation in form of inner supra-orbital spine rudiment, (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped. Scale = 0.1 mm.

MYSIS. In each substage, the carapace bears a distinctive series of spines or serrations along its anteroventral border (Fig. $11b_1$). The rostrum, down-curved, extends beyond eye. All mysis substages have supraorbital and pterygostomial spines. Small hepatic spine may be absent in 1st substage but always present afterwards. Dorsal spines sometimes on 4th abdominal segment, always on 5th and 6th, and lateral spines on 5th and 6th segments.

Mysis I of *M. palmensis* (Table 2, Fig. 11) retains 1 pair of supraorbital spines; rostrum has

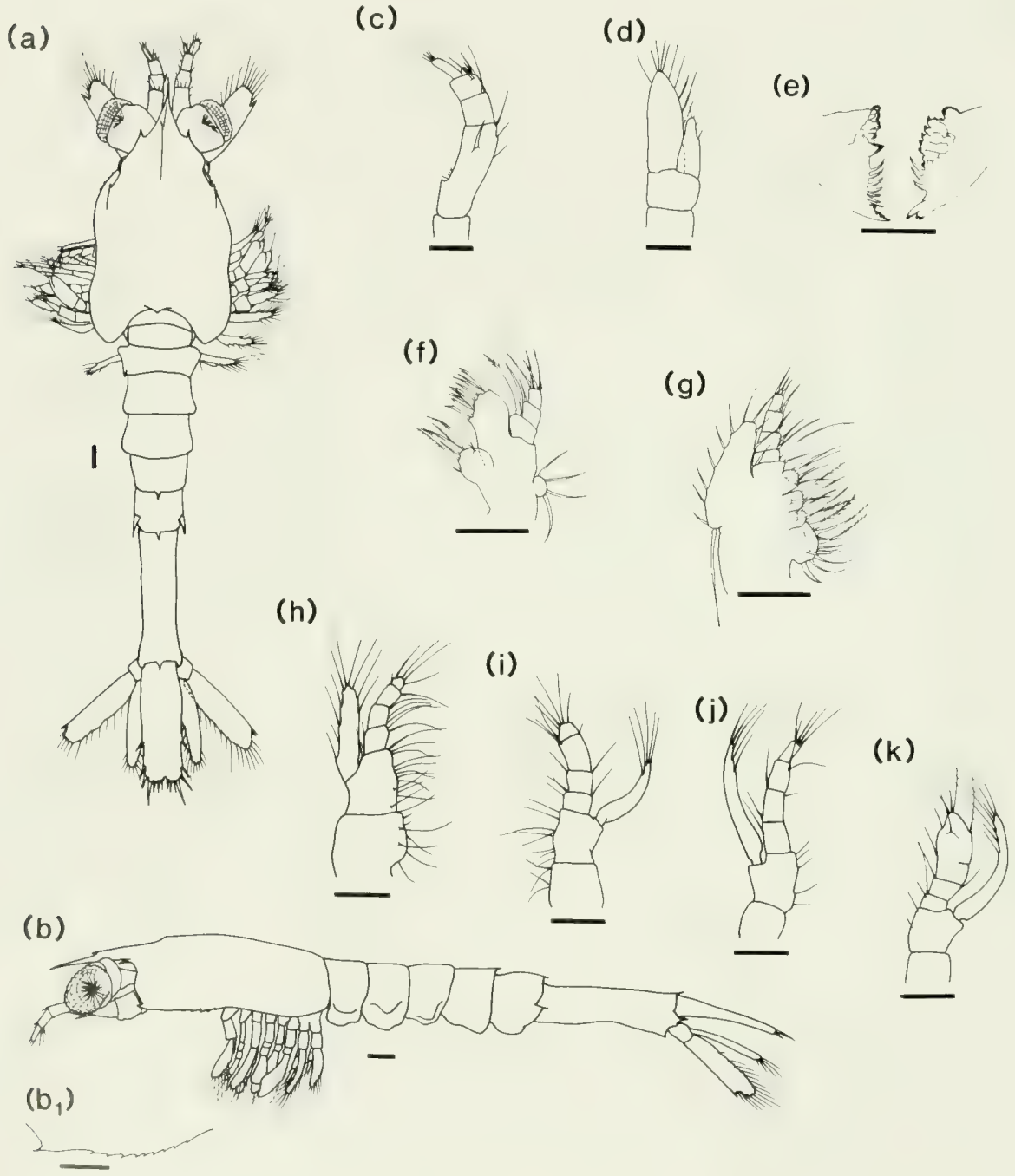

FIGURE 11.—*Metapenaeopsis palmensis* mysis I. (a) whole animal (dorsal view), (b) whole animal (lateral view), (b_1) detail-serrated anteroventral carapace margin, (c) 1st antenna, (d) 2nd antenna, (e) mandibles, (f) 1st maxilla, (g) 2nd maxilla, (h) 1st maxilliped, (i) 2nd maxilliped, (j) 3rd maxilliped, (k) 1st pereopod. Scale = 0.1 mm.

at most 1 dorsal tooth; small hepatic spine sometimes present (Fig. 11a, b). Epipod of 2nd maxilla (Fig. 11g) more enlarged than that of *A. formosus* at same substage. Mysis II (Fig. 12) with 2 dorsal rostral teeth, hepatic spine always present (Fig. 12a). In contrast to *A. formosus*, still no statocyst in 1st antenna (Fig. 12b), but 2nd antennal flagellum already as long as blade (Fig. 12c). Posterior border of telson with only slight cleft, and small median spine (telson formula now 7+1+7) (Fig. 12k). Mysis III (Fig. 13) with 2 or 3 dorsal rostral teeth and an epigastric tooth. First antenna now usually with a small statocyst (Fig. 13b); 2nd antennal flagellum longer than blade (Fig. 13c). Mandibles with unsegmented palp (Fig. 13d). Telson notch absent, posterior margin slightly rounded. Median spine still very short (Fig. 13k).

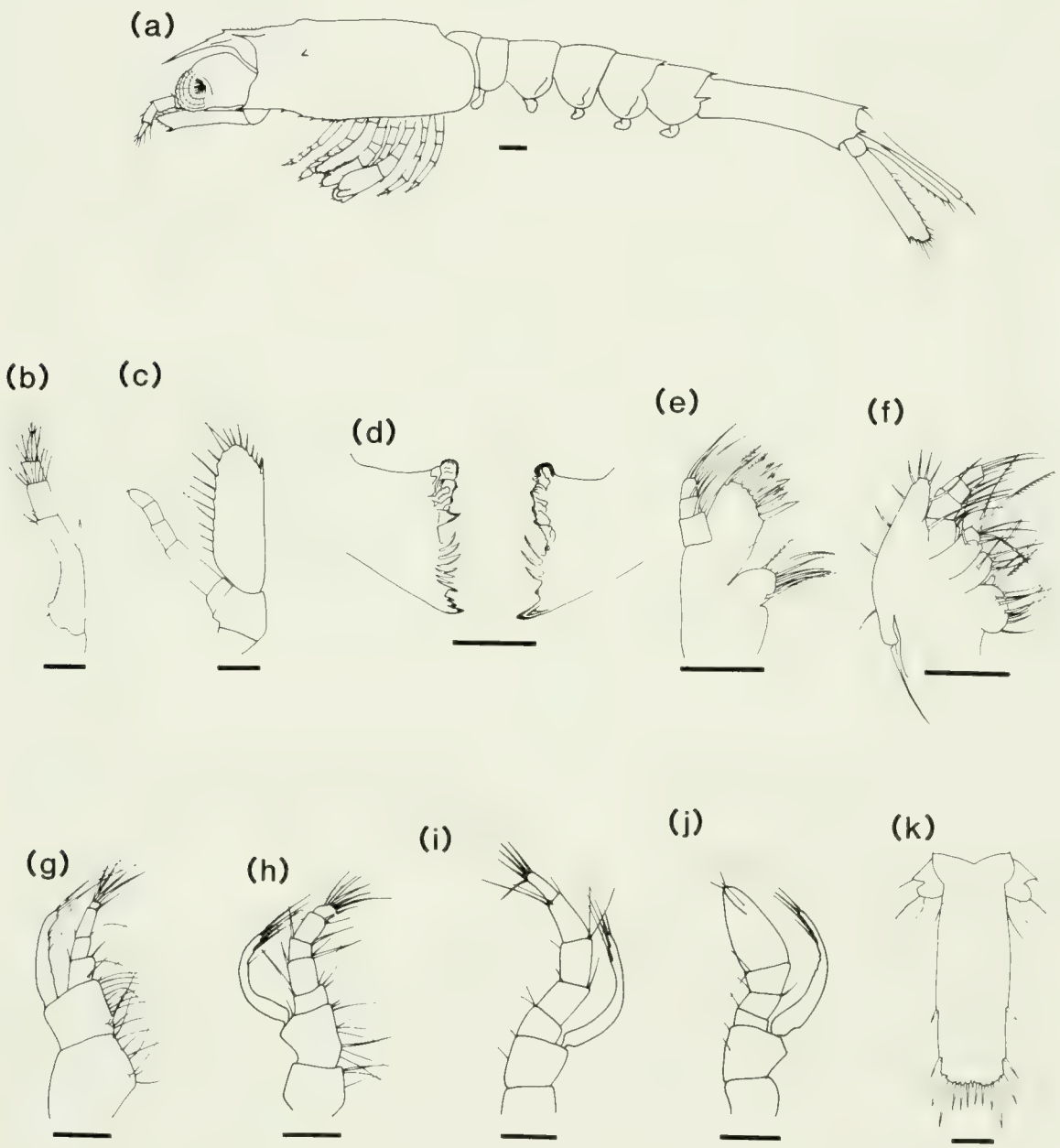

FIGURE 12.—*Metapenaeopsis palmensis* mysis II. (a) whole animal (lateral view), (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped, (j) 1st pereopod, (k) telson. Scale = 0.1 mm.

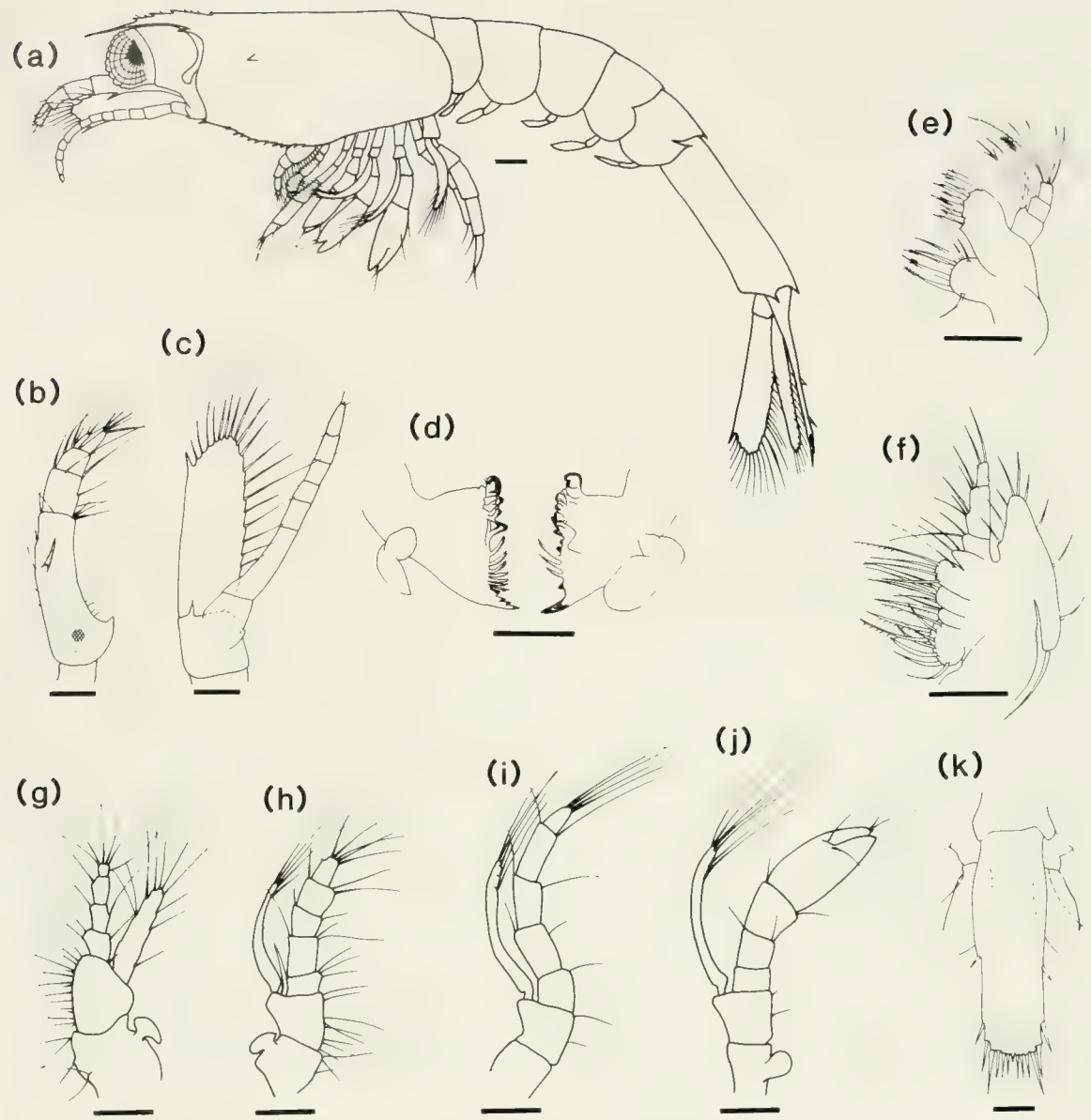

FIGURE 13.—*Metapenaeopsis palmensis* mysis III. (a) whole animal (lateral view), (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped, (j) 1st pereopod, (k) telson. Scale = 0.1 mm.

POSTLARVA. The postlarva of *M. palmensis* (Table 2, Fig. 14) lacks the supraorbital spines and carapace serrations of the mysis substages. Pterygostomial spine and hepatic spine remain, now also a small antennal spine (Fig. 14a). Rostrum slightly shorter than eye, with 3 or 4 dorsal teeth and an epigastric tooth (Fig. 14a). First antenna lacking distal spine which *A. formosus* bears on proximal segment. Two small sternal spines on 1st thoracic segment, 2 long spines on 2nd thoracic segment (thoracic sternal spine formula 2+2+0+0+0) (Fig. 15d). Abdominal spination reduced, only 1 dorsal spine on 6th segment. Posterior margin of telson more V-shaped, spine formula remaining 7+1+7 (Fig. 14k). Median spine now large. Telson also bearing 3 or 4 small setae on each side of its posterior margin.

Generic Characteristics of Penaeid Larvae

The distribution of setae on the protopod and

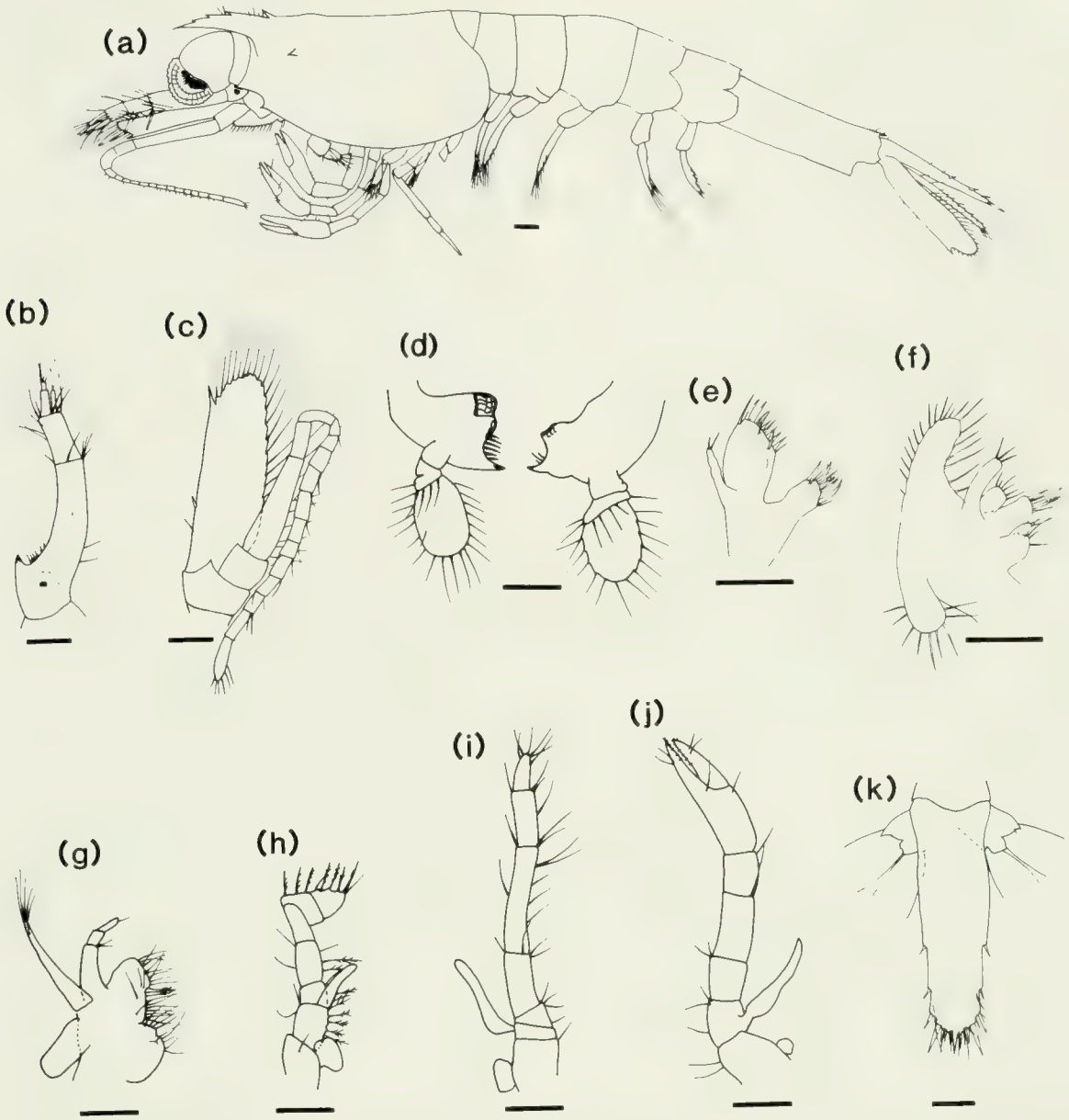

FIGURE 14.—*Metapenaeopsis palmensis* postlarva. (a) whole animal (lateral view), (b) 1st antenna, (c) 2nd antenna, (d) mandibles, (e) 1st maxilla, (f) 2nd maxilla, (g) 1st maxilliped, (h) 2nd maxilliped, (i) 3rd maxilliped, (j) 1st pereopod, (k) telson. Scale = 0.1 mm.

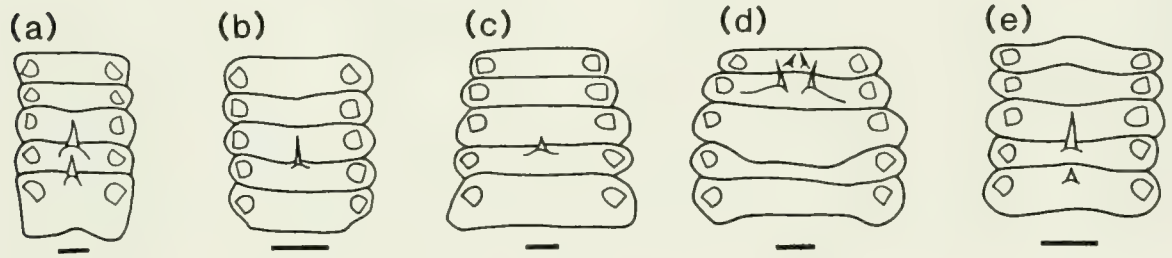

FIGURE 15.—Thoracic sternal spine distribution of postlarvae. (a) *Penaeus* (except for subgenus *Litopenaeus*; see text), (b) *Metapenaeus*, (c) *Trachypenaeus*, (d) *Metapenaeopsis*, (e) *Atypopenaeus*. Scale = 0.1 mm.

endopod of the 2nd antenna has been used for generic identification of protozoea (Cook 1966a; Hassan 1974; Haq and Hassan 1975). While this character is often referred to as the setal formula of the 2nd antennal endopod, this is not correct as the first seta referenced arises from the protopod.

We compared the 2nd antennal formulae of protozoeae in our reference collection with published formulae. All *Penaeus* larvae in our collection have the formula 1+1+2, in agreement with other published descriptions. The three species of *Trachypenaeus* in our collection (*T. anchoralis*, *T. fulvus*, and *T. granulosus*) have the formula 0+2+2, which is in agreement with the only existing published descriptions by Kirkegaard (1969) and Pearson (1939). *Parapenaeopsis* is represented in our reference collection by the protozoeae of *P. cornuta*, which also have the formula 0+2+2. This confirms the formula found by Hassan (1984) for *P. stylifera*. Rao (1973) also described larvae of *P. stylifera*, and his figures seem to indicate the same formula of 0+2+2, although no detailed drawings of appendages are provided.

However, the 2nd antennal formula is not consistent in all genera. There are five species of *Metapenaeus* in our reference collection: *M. bennettae*, *M. eborocensis*, *M. endeavouri*, *M. ensis*, and *M. insolitus*. These larvae normally have the formula 1+2+3, but on some occasions the formula is 1+2+2. This difference occurs at random (although rarely) among most species. Menon (1951), Morris and Bennett (1951), Raje and Ranade (1972), Kurata and Vanitchkul (1974), Courties (1976), and Hassan (1980) agreed that *Metapenaeus* have 1+2+2, while Vanitchkul (1970), Hassan (1974), and Haq and Hassan (1975) found both 1+2+2 and 1+2+3. In our larvae, the third seta in the most distal group was often small and hard to distinguish when present, and could easily have been overlooked. Similarly, the 2 species of *Metapenaeopsis* we have reared are not consistent. *Metapenaeopsis palmensis* is always 1+2+2, but *M. novaeguinae*, although normally exhibiting the same formula, occasionally has 1+2+3.

In the mysis stage, the presence of a serrate anteroventral carapace margin (Fig. $11b_1$) is a character that has not previously been described for laboratory-reared penaeid larvae. At present the only genus in which it is definitely present is *Metapenaeopsis*—both *M. palmensis* and *M. novaeguinae* from our reference collection.

The number and placement of thoracic sternal spines have not been mentioned in previous studies. In cleared and stained specimens it is an easy character to assess and makes postlarval identification straightforward, and it is an important generic character in our key for postlarvae. Unfortunately these spines have not been described by other workers and so we have no information about the sternal spine formulae for genera that are not represented in our reference collection. Partly owing to this we have used other characters to help identify some genera; however, when both the size and position of the sternal spines are taken into account, they are sufficient to identify five genera: *Atypopenaeus*, *Metapenaeopsis*, *Metapenaeus*, *Penaeus*, and *Trachypenaeus* (Fig. 15). Within the genus *Penaeus*, the sternal spine formula has taxonomic value at the subgenus level. We have examined postlarvae from 3 species within the subgenus *Litopenaeus* (*P. setiferus*, *P. stylirostris*, and *P. vannamei*), all of which have only a single, small sternal spine on the 4th segment (formula 0+0+0+1+0). All other *Penaeus* examined have a large spine on the 4th segment and a small spine on the 5th (formula 0+0+0+1+1): *P. aztecus* from the subgenus *Farfantepenaeus*; *P. indicus* and *P. merguiensis* from the subgenus *Fenneropenaeus*; *P. japonicus* from the subgenus *Marsupenaeus*; *P. latisulcatus*, *P. longistylus*, and *P. plebejus* from the subgenus *Melicertus*; and *P. esculentus*, *P. monodon*, and *P. semisulcatus* from the subgenus *Penaeus*. Species of *Litopenaeus* do not occur in the Indo-west Pacific region and so will not be wrongly identified by our key.

We have not used the distribution of abdominal spines in protozoea III or mysis substages (e.g., Cook 1966a; Muthu et al. 1978), since their presence can be variable, at least for *M. palmensis*. Paulinose (1977) suggested that the dentition and asymmetry of the mandibles might be useful for both generic and specific identification of penaeid larvae. We have not investigated this possibility since the operational use of this character would not be practical due to the time-consuming dissections necessary.

Key to Penaeid Genera

Our key was constructed from both our own reference collection and published descriptions. Many species were referred to in characterizing the genera *Penaeus*, *Metapenaeus*, and *Trachypenaeus*. However, there is much less reference material available for other genera. Although

Metapenaeopsis has more species than any other penaeid genus found in the Indo-west Pacific region (Dall et al. in press), our key is based on just 2 species, both from our own reference collection. Characteristics of the genera *Atypopenaeus*, *Parapenaeopsis*, and *Parapenaeus* have been based on a single species. For this reason, and because the genera *Heteropenaeus*, *Trachypenaeopsis*, and *Penaeopsis* have been omitted, the key must be regarded as provisional, and subject to revision as more descriptions are published.

The protozoeae of *Metapenaeus*, *Atypopenaeus*, and *Metapenaeopsis*, and *Parapenaeus* are very similar. For protozoea II and III, distinction between these genera relies on the shape of the telson, rostrum, and supraorbital spines. These characters should be assessed with reference to Figures 17 and 18 and, if there is any doubt, the suite of characteristics in Table 3. In most cases the characters used in the key should be sufficient to identify mysis larvae and postlarvae without difficulty. However, as an additional check, the general shape of the antennal blades is a useful generic character, and should be compared with those shown (Fig. 16).

The family Penaeidae no longer includes members of the Aristaeidae, Solenoceridae, Sergestidae, or Sicyoniidae; these are now separate families within the superfamily Penaeoidea (Bowman and Abele 1982). We have restricted our key to the family Penaeidae. However, lar-

TABLE 3.—Characteristics of protozoeal stages of the genera *Atypopenaeus*, *Metapenaeopsis*, *Metapenaeus*, and *Parapenaeus*. Sources of information: *Atypopenaeus*, *Metapenaeopsis*, *Metapenaeus*—present study and reference collection of larvae held by the authors; additional sources for *Metapenaeus* species—see Dall et al. (in press) for review; specific sources referenced in table—*Parapenaeus stylifera* – [1]Heldt 1938, [2]Pearson 1939; *Metapenaeus monoceros* – [3]Courties 1976, [4]Raje and Ranade 1972.

	Atypopenaeus	*Metapenaeopsis*	*Metapenaeus*	*Parapenaeus*
Protozoea I				
Number of setae on 2nd antenna exopod inner margin	9-10	9-11	10	11
2nd antennal setal formula	1+2+2	1+2+2 or 1+2+3	1+2+2 or 1+2+3	0+2+2[1] or 1+2+2[2]
Anterior carapace	no spines	long spines	short spines except none for *M. ensis*, *M. monoceros*[3,4]	long spines
Protozoea II				
Number of setae on 2nd antenna exopod inner margin	9-10	9-11	10	11
2nd antennal setal formula	1+2+2	1+2+2 or 1+2+3	1+2+2 or 1+2+3	1+2+2[1] or 1+2+3[2]
Rostrum	longer than eye	longer then eye, curved	about eye length	longer than eye
Supraorbital spines	one	two similar size	one except for *M. ensis*, *M. monoceros*[3,4] (inner much smaller than outer)	two similar size
Protozoea III				
Number of setae on 2nd antenna exopod inner margin	9-10	10-11	10	11[2] or 12[1]
2nd antennal setal formula	1+2+2	1+2+2 or 1+2+3	1+2+2 or 1+2+3	0+2+2[1] or 1+2+3[2]
Rostrum	longer than eye	longer than eye, curved	about eye length	longer than eye
Supraorbital spines	one	one plus rudiment of second (Fig. 10a_1)	one	two (inner smaller than outer)
Telson spines	7+7	7+7	7+7	8+8

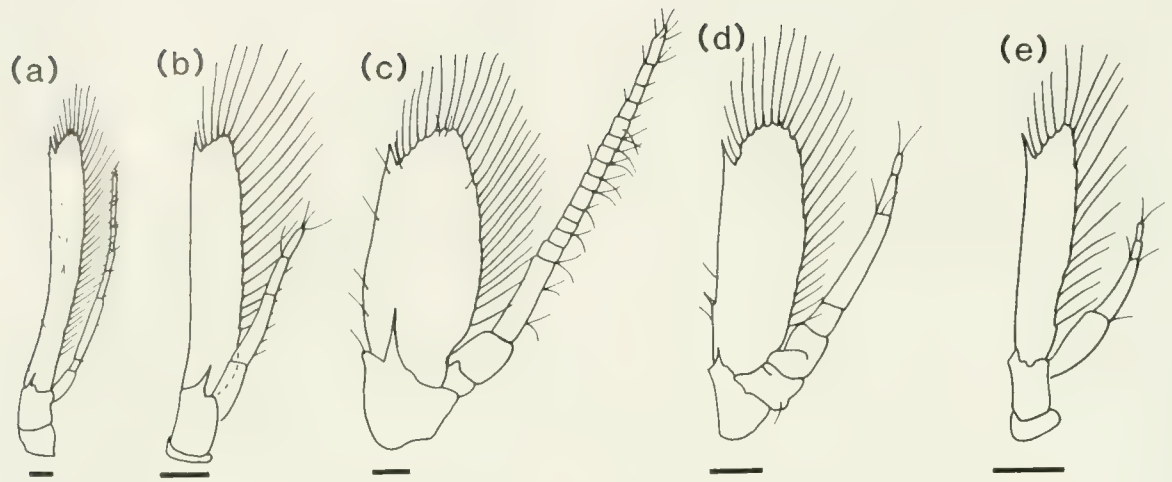

FIGURE 16.—Second antenna of postlarvae. (a) *Penaeus*, (b) *Metapenaeus*, (c) *Trachypenaeus*, (d) *Metapenaeopsis*, (e) *Atypopenaeus*. Scale = 0.1 mm.

vae from other families within the superfamily Penaeoidea might occur with penaeids. Characteristics that can identify larvae of related families are described by Cook (1966a) and Dall et al. (in press).

The key is not useful for later postlarval stages. It is difficult to define the cutoff point for older postlarvae, but the following characteristics may indicate that the postlarva is too old for accurate identification: there are more than 4 rostral spines; the antennal flagellum is longer than half the body length; the telson has a pronounced V-shape; and there are many setae on the telson.

Key

Protozoea

1 Setal formula on 2nd antennal protopod and endopod 1+1+2 ..... *Penaeus*
2nd antennal formula 0+1+2 ..... *Macropetasma*
2nd antennal formula not 1+1+2 or 0+1+2 2

2(1) 2nd antennal formula 0+2+2 3
2nd antennal formula 1+2+2 or 1+2+3 5

3(2) 2nd antennal exopod with 11 setae on inner margin ..... *Parapenaeus*
2nd antennal exopod with 10 setae on inner margin 4

4(3) Dorsal surface of carapace with small hump; telson notch moderately wide (Fig. 17c, i) ..... *Trachypenaeus*
Dorsal surface of carapace smooth; telson notch very wide (Fig. 17f, l) ..... *Parapenaeopsis*

5(2) Eyes immobile (protozoea I) 6
Eyes mobile (protozoea II or III) 9

Protozoea I

6(5) Strong spines above frontal organs, length at least 0.7 of 1st antenna diameter (Fig. 8a) ..... *Metapenaeopsis*
Spines above frontal organs small or missing 7

7(6) 2nd antennal exopod with 11 setae on inner margin ..... *Parapenaeus*
2nd antennal exopod with 10 setae on inner margin 8

8(7) Carapace about 0.5 of total length; usually small spines above frontal organs ..... *Metapenaeus*
Carapace about 0.4 of total length; no spines above frontal organs ..... *Atypopenaeus*

9(5) Uropods absent (protozoea II) 10

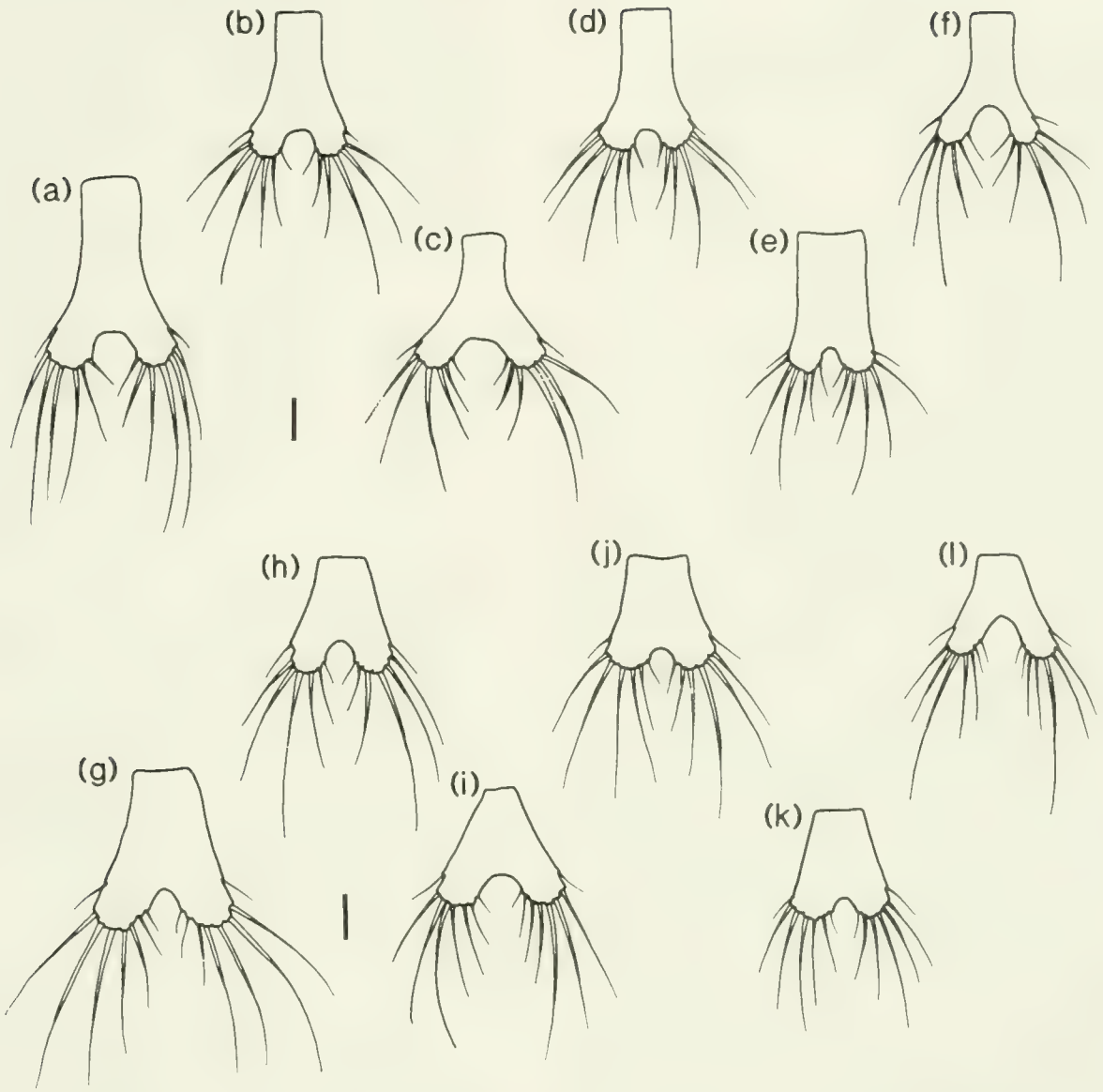

FIGURE 17.—Telson shapes of protozoeae. Protozoea II – (a) *Penaeus*, (b) *Metapenaeus*, (c) *Trachypenaeus*, (d) *Metapenaeopsis*, (e) *Atypopenaeus*, (f) *Parapenaeopsis*. Protozoea III – (g) *Penaeus*, (h) *Metapenaeus*, (i) *Trachypenaeus*, (j) *Metapenaeopsis*, (k) *Atypopenaeus*, (l) *Parapenaeopsis*. Scale = 0.1 mm.

Uropods present (protozoea III)..... 14

Protozoea II

10(9) A single pair of supraorbital spines (Fig. 2a)..... 11
Two pairs of supraorbital spines (Fig. 9a)..... 12

11(10) Telson wedge-shaped, with no distinct angle in lateral border (Fig. 17e)..... *Atypopenaeus*
Telson with a distinct angle in lateral border (Fig. 17b) ..... *Metapenaeus*

12(10) Inner pair of supraorbital spines filamentous and less than half as long as outer pair (Fig. 18)..... *Metapenaeus*[3]
Inner pair of supraorbital spines robust, similar in size to outer pair (Fig. 9a)..... 13

13(12) Body length greater than 1.6 mm .... *Parapenaeus*
Body length less than 1.6 mm..... *Metapenaeopsis*

[3] *M. ensis* or *M. monoceros*.

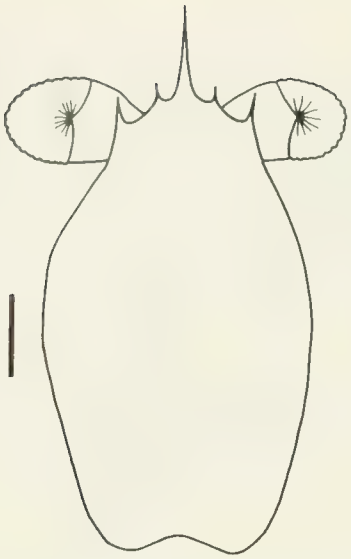

FIGURE 18.—Carapace of *Metapenaeus ensis* protozoea II. Scale = 0.1 mm.

Protozoea III

14(8) A single supraorbital spine, with straight carapace border between supraorbital spine and rostrum (Fig. 3a) 15
2 supraorbital spines, or 1 supraorbital spine with 1 or 2 small denticles, or a protrusion in carapace border between supraorbital spine and rostrum (Fig. $10a_1$) 16

15(14) Rostrum about same length as eye ... . *Metapenaeus*
Rostrum about 1.5 times eye length .. .. *Atypopenaeus*

16(14) Two well-defined supraorbital spines . ..... *Parapenaeus*
One supraorbital spine with 1 or 2 small denticles, or a protrusion in carapace border between supraorbital spine and rostrum (Fig. 10b) .... *Metapenaeopsis*

Mysis

1 Anteroventral margin of carapace serrated (Fig. $11b_1$) ..... *Metapenaeopsis*
Anteroventral margin of carapace smooth 2

2(1) 3rd abdominal segment with large dorsal spine; abdomen permanently flexed at 3rd abdominal segment (Fig. 19c) .. .. *Parapenaeus*
3rd abdominal segment with no spine or a small spine; no permanent flexion of abdomen 3

3(2) 5th abdominal segment with a large dorsal spine, equal in length to diameter of segment (Fig. 19a) .... *Macropetasma*
5th abdominal segment with no spine or with a spine of length less than half diameter of segment 4

4(3) Telson spine formula 8+8 5
Telson spine formula 7+7 7

5(4) Hepatic spine present ..... *Penaeus*
Hepatic spine absent 6

6(5) Rostrum very short, less than half eye length ..... *Trachypenaeus*
Rostrum longer than half eye length .. .. *Parapenaeopsis*

7(4) Rostrum down-curved, longer than eye ..... *Atypopenaeus*
Rostrum straight, shorter than eye... ..... *Metapenaeus*

Postlarva

1 3rd abdominal segment with large dorsal spine; abdomen permanently flexed at 3rd abdominal segment (Fig. 19d) ..... *Parapenaeus*
3rd abdominal segment with no spine or a small spine; no permanent flexion of abdomen 2

2(1) Rostrum with more than one dorsal tooth 3
Rostrum with zero or one dorsal teeth ..... *Macropetasma*

3(2) Telson with a median spine 4
Telson without a median spine 5

4(3) Telson with 8+1+8 spines .... *Parapenaeopsis*
Telson with 7+1+7 spines; thoracic sternal spine formula 2+2+0+0+0 (Fig. 15d) ..... *Metapenaeopsis*

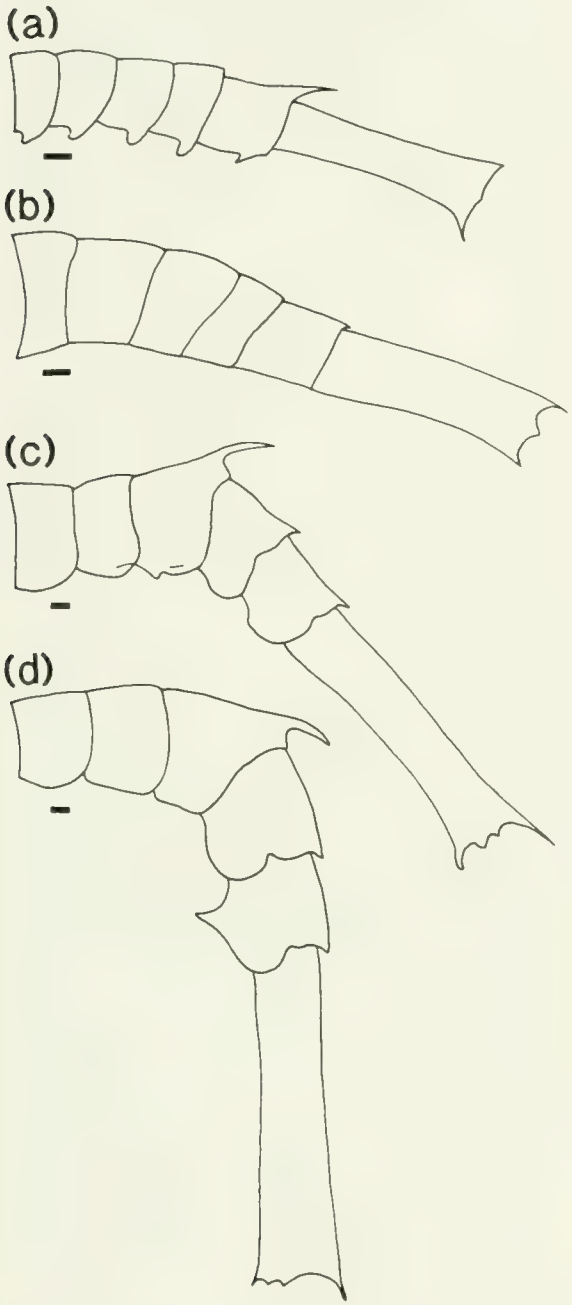

FIGURE 19.—Abdomen of *Macropetasma* (a) mysis II, (b) postlarva (redrawn from Cockcroft 1985) and *Parapenaeus* (c) mysis II, (d) postlarva (redrawn from Heldt 1938). Scale = 0.1 mm.

5(3) Telson with 8+8 spines 6
Telson with 7+7 spines 7

6(5) Thoracic sternal spine formula 0+0+0+1+1 (Fig. 15a) ..... *Penaeus*
Thoracic sternal spine formula 0+0+0+1+0 (Fig. 15c) ..... *Trachypenaeus*

7(5) Thoracic sternal spine formula 0+0+0+1+0 (Fig. 15b) ..... *Metapenaeus*
Thoracic sternal spine formula 0+0+0+1+1 (Fig. 15e) ..... *Atypopenaeus*

DISCUSSION

Previous Descriptions of Penaeid Larvae

The only way to describe the morphology and to be certain of the identity of penaeid larvae is to rear them in the laboratory, beginning with eggs from adults of known identity. Techniques for inducing penaeids to spawn and for culturing the larvae have been known for many years (Hudinaga 1942). For the genera *Penaeus* and *Metapenaeus* there are over 30 descriptions of larvae whose identity is certain (Dall et al. in press). Laboratory-reared larvae of other penaeid genera, also commercially important, are less well described. There are only a few useful descriptions of any species of *Parapenaeopsis* (Hassan 1984; Rao 1973), *Parapenaeus* (Heldt 1938; Pearson 1939) or *Trachypenaeus* (Pearson 1939; Kirkegaard 1969, protozoea I only), and this study is the first description of any species of *Metapenaeopsis* or *Atypopenaeus* based on laboratory-reared material.

Many workers have attempted to describe particular species or genera of penaeid larvae, based solely on planktonic material (see Dall et al. in press, for review). However the morphology of penaeid larvae undergoes major changes between each stage: egg to nauplius, nauplius to protozoea, and protozoea to mysis. Even between the protozoeal substages, changes are so great as to defy any attempt to link one substage with the next. A full larval life history cannot, we believe, be accurately reconstructed from larvae caught from the plankton unless at least some substages are subsequently reared (as in Pearson 1939).

The presence of commercial fisheries for a certain species is also a poor guide to the identity of larvae found in the same area. There may be significant populations of penaeid genera present that are not, for various reasons (small size, untrawlable habitat), represented in commercial catches. Larvae also have considerable potential for advection up to 150 km (Rothlisberg 1982; Rothlisberg et al. 1983b).

In several older studies, workers based their identification of larvae from the plankton on the temporal or spatial distribution of the adult

prawns, and were later found to be in error. For example, Heegard (1953) identified larvae from plankton collections as *Penaeus setiferus*. However, the protozoea I figured has a 2nd antennal setal formula of 0+2+2 and a wide telson notch, characters not seen in *Penaeus* but consistent with either *Trachypenaeus* or *Parapenaeopsis*. The protozoea II figured has the same 2nd antennal setal formula as the protozoea I, and the form of the rostrum and supraorbitals are not characteristic of *Penaeus*. However, this substage has supraorbital spines, which *Trachypenaeus* and *Parapenaeopsis* larvae do not. Heegard's protozoea III is consistent with *Penaeus* in some respects, such as the long rostrum, but its 2nd antennal setal formula is now 1+2+2, whereas the *Penaeus* formula is 1+1+2. It is likely that the protozeae described are from several genera, although the figures do not show sufficient detail for an accurate identification. On the other hand, Heegard's mysis figures are generally consistent with *Penaeus*, although the specific identification is in doubt since *P. aztecus*, *P. duorarum*, and *P. setiferus* all exist in the collection area. Similarly Dakin (1938) identified plankton-caught larvae as *P. plebejus*, but they were probably a combination of *Trachypenaeus* (based on the relative lengths of the 1st and 2nd antennae of protozoea III) and *Metapenaeus* (a 2nd antennal setal formula of 1+2+3 and telson with 7+7 spines in protozoea III). As a final example, Subramanyam (1965) reported a high density of penaeid eggs in the plankton off the Madras coast, and identified them as *P. indicus* after culturing several nauplius substages. However, the large egg diameter (0.45 mm) and large perivitelline space indicate that the eggs were probably *Trachypenaeus*, since *Penaeus* eggs have a diameter between 0.23 mm and 0.31 mm and a narrow perivitelline space (Dall et al. in press).

Descriptions of the lesser known penaeid genera from plankton samples may also be based on mistaken identifications. The only published description of larvae of the genus *Penaeopsis* is of *P. rectacuta* (Paulinose 1973), but the author gave no support for his choice of genus. The larvae were collected from areas of the Indian Ocean where species of other previously undescribed genera are common, including *Atypopenaeus stenodactylus*, *Metapenaeopsis andamensis*, *M. barbata*, *M. hilarula*, *M. mogiensis*, *M. philippii*, and *M. stridulans*, all of which are sufficiently abundant to support some commercial fishing (Dall et al. in press). The present description of *Metapenaeopsis palmensis* has much in common with several of the substages described by Paulinose (1973). The 2nd antennal formula of 1+2+2, a reduced second supraorbital spine in protozoea III, the rostrum length, the shape and spination of the mysis, and the serrate anteroventral carapace margin of the mysis substages are all consistent with *M. palmensis* described in the present study. Protozoea II is probably from a different genus, since it has no supraorbital spines [in all penaeids described except *Macropetasma africanum* (Cockcroft 1985) the presence or absence of supraorbital spines is the same for both protozoea II and III]. However, the figure of this substage shows the 2nd antennal exopod (on the whole animal) as symmetrical, with about 9 setae along both the interior and the exterior borders, whereas the drawing of the dissected appendage shows the more typical penaeid form of 10 setae along the inner border and 2 on the outer border. More subtle characters may also have been represented incorrectly, so confident identification is difficult; however, the characteristics shown (lack of supraorbital spines, a deep and wide telson notch and a relatively short rostrum) are consistent with both *Trachypenaeus* and *Parapenaeopsis*.

Paulinose (1986) described mysis I and II and an early postlarva (which, because of lack of setae on the pleopods, we call mysis III) from the Indian Ocean. He tentatively identified it as *Atypopenaeus stenodactylus*. However, these larvae resemble our *Metapenaeopsis palmensis* and differ from our *A. formosus* in the following important characters: rostrum length and shape (long and curved); the presence of a serrated anteroventral carapace margin; telson spine formula (7+7 for mysis I, 7+1+7 for mysis II and III) and abdomen spination (dorsal spines on the fourth, fifth, and sixth segments and lateral spines on the fifth and sixth segments). Although there are some differences between *M. palmensis* and the larvae described by Paulinose (1986), we feel that these larvae are not *Atypopenaeus* but most likely an unidentified species of *Metapenaeopsis*.

Most recently, Paulinose (1988) described mysis and postlarval stages of *Metapenaeopsis mogiensis*, *M. andamanensis*, and *M. barbata* from widely spread locations in the Indian Ocean. Unfortunately, genus and species were again assigned by comparison with known distributions of adult prawn species, and by linking substages based on similarity of appearance.

While the larvae have many similarities, there were two important characters missing from the *M. palmensis* described here, which Paulinose claims to be diagnostic for the genus: a dentate postero-inferior carapace margin, and serrated abdominal pleura. Given the large number of *Metapenaeopsis* species, these characters may vary within the genus.

Morphological Variation

The larval descriptions given in this study were based on a number of individuals sampled, where possible, from a number of spawnings. However, previous studies have shown that with the degree of intraspecific variation in morphology, hundreds of larvae from many spawnings should be examined, and each substage should be sampled several times to account for intramolt growth (Rothlisberg et al. 1983a; Jackson 1986). In this study, there was insufficient material for such exhaustive examination, and so the full range of variations may not be described.

Some morphological variation can be induced by environmental factors such as salinity and temperature (Jackson 1986), and the special environment of the laboratory may do the same. In an unsuitable laboratory environment, obvious deformities can occur (Rao and Kathirval 1973), and less extreme environmental conditions may result in more subtle morphological effects. Therefore, while in this study much emphasis has been placed on laboratory rearing as a means of ensuring correct larval identification, more work is needed to discover to what degree laboratory-reared larvae differ from those in the natural environment. Differences between field-caught and laboratory-reared larvae have been found for the carid shrimp *Pandalus jordani* (Rothlisberg 1980), both in morphology and in the number of substages.

While many workers have searched for taxonomic characters to separate species of penaeid larvae within genera, they have generally been unsuccessful (Cook 1966b; Cook and Murphy 1971; Courties 1976). The only reliable way of distinguishing species of larval penaeids is to make a discriminant analysis of a number of morphological characters (Rothlisberg et al. 1983a; Jackson 1986). Discriminant analysis is less successful for postlarvae, and a technique based on electrophoresis is being developed (Lavery and Staples in press). The descriptions presented in this study are therefore of limited value in species identification.

Keys to the Genera of Larval Penaeids

The genera *Penaeus*, *Metapenaeus*, *Parapenaeopsis*, *Parapenaeus*, *Trachypenaeus*, *Metapenaeopsis*, *Atypopenaeus*, *Penaeopsis*, *Funchalia*, *Trachypenaeopsis*, *Sicyonica*, *Aristaeomorpha*, and *Solenocera* are included in Paulinose's (1982) key to penaeid larvae. Reconstructions of larval series from plankton collections were used as reference material for most of the genera. The protozoea key uses the length of the rostrum, the distribution of dorsal abdominal spines and the number of telson setae without qualifying these characters according to the substage. Most protozoeae would not be identified correctly because protozoea I does not have a rostrum; only protozoeae III have dorsal abdominal spines; and telson spines in *Penaeus*, *Trachypenaeus*, *Parapenaeopsis*, *Macropetasma*, and *Parapenaeus* vary in number between protozoea II and protozoea III. In the mysis key, *Atypopenaeus* are identified by a telson setal formula of 7+1+7, although the present study shows *A. formosus* has 7+7. *Metapenaeopsis* mysis larvae are said to have the pleura of the first five abdominal segments serrated ventrally, a characteristic not found in *M. palmensis* in the present study.

This is the first generic key for the Indo-west Pacific penaeid larvae that relies on descriptions of laboratory-reared larvae. Relying on laboratory rearings restricted the number of descriptions and species available for reference, but we feel this was justified by the improved precision obtained. In the present study, it was not possible to include *Funchalia*, *Heteropenaeus*, *Penaeopsis*, or *Trachypenaeopsis*, as no laboratory-reared larvae of these genera have been described. Owing to their rarity, the omission of three of these will have little effect on the practical application of the key. The fact that *Penaeopsis* is not included is more unfortunate since this genus is relatively abundant (Dall et al. in press). The key will be enhanced when larvae from the above genera are reared, as well as more species of *Atypopenaeus*, *Metapenaeopsis*, *Parapenaeopsis*, *Parapenaeus*, and *Trachypenaeus*. We have reared several species of *Trachypenaeus* and are preparing descriptions of *T. fulvus* larvae to compare with other *Trachypenaeus* species in our reference collection.

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Studying marine larval ecology and physiology is difficult: laboratory studies, requiring larval culture, are only now becoming routine, and field studies are fraught with taxonomic and sampling problems. Combined laboratory and field studies that provide real insight into the factors that affect larval distribution, abundance, and survival are that much more difficult and rare. Dr. Reuben Lasker and his group were pioneers and pre-eminent in this integrated approach. Taxonomic studies such as the present work are the basis for such research, which is only now beginning on tropical penaeids. We dedicate this paper to Reuben's inspiring example.

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Larvae of *Liparis fucensis* and *Liparis callyodon*: Is the "Cottoid Bubblemorp" Phylogenetically Significant?

Jeffrey B. Marliave and Alex E. Peden

ABSTRACT: Larvae of the slipskin snailfish, *Liparis fucensis*, and of the spotted snailfish, *Liparis callyodon*, are described; and fecundity/spawning information for these species is provided. Positive identification of larvae of both species required that they be laboratory reared up to identifiable juvenile stages. Too little taxonomic information exists on larvae of this genus to reveal diagnostic characters for northeast Pacific species. The early development patterns of these two species are contrasted; *L. fucensis* larvae grow from a very small to a very large size during the larval stage, and develop an enlarged subdermal space, the "cottoid bubblemorph", whereas *L. callyodon* larvae develop more typically. Evidence from the literature indicates that this bubble morphology is a convergent, derived character, and is unsuitable for use in determining phylogenetic relationships.

Larval descriptions do not exist for any of the 17 species of the genus *Liparis* that occur in the northeast Pacific Ocean (Matarese et al. in press), except for illustrations of newly hatched *Liparis fucensis* (Marliave 1975). Larvae of the subfamily Liparidinae were discussed generally by Able et al. (1984), with emphasis primarily on pigment and ontogenetic schedule of developmental landmarks. Able et al. (1984) included an illustration (their figure 236 bottom) of an unidentified cyclopterid from southern California with an enlarged cranial and thoracic subdermal space giving a bubble appearance, and suggested that such a feature might be of taxonomic value. Another cottoid larva sharing this bubble appearance is *Malacocottus zonurus* (Washington et al. 1984). This type of anomalous morphological feature of a larval fish must be considered as a possible character for elucidating phylogenetic relations (Kendall et al. 1984), and the extent to which such a feature is conservative, as opposed to immediately adaptive, is fundamental to assessing the utility of such a feature as a phylogenetic character (Cohen 1984). Thus, Haeckel's biogenetic law, that ontogeny recapitulates phylogeny, becomes a moot theory with developmental stages as intensely subjected to selective pressures as the planktonic larval stages of fish. This paper provides insight regarding the presence (*fucensis*) versus absence (*callyodon*) of the larval cottoid bubblemorph in two closely related, sympatric *Liparis* species.

Adults of slipskin snailfish, *L. fucensis*, and spotted snailfish, *L. callyodon*, look very similar and are close in morphometrics and meristics (Clemens and Wilby 1961; Hart 1973). *Liparis fucensis* is distributed over a greater depth range than the shallow-water *L. callyodon* (Clemens and Wilby 1961); but they do overlap in shallow water. Spawning in *L. fucensis* involves the male tending egg masses deposited among polychaete worm tubes (Marliave 1975) or inside empty mussel shells (DeMartini 1978) in shallow subtidal waters. No information has been published previously regarding reproduction of *L. callyodon*.

Two different approaches for obtaining larval specimens—captive rearing and plankton towing—provided developmental series for these two species. Both species were reared through transformation to the juvenile stage, permitting positive identification. This paper provides the first larval descriptions for northeast Pacific *Liparis* species. The bubble morphology of *L. fucensis* larvae is constrasted with the more typical larval morphology of *L. callyodon*.

METHODS

Eggs and a 67 mm ripe male of *L. fucensis* were collected at a depth of 10 m from among the tubes of *Eudistylia polymorpha* by divers in Barkley Sound, British Columbia (lat. 48°50′N, long. 125°08′30″W) on 26 May 1974. The embryos were not visibly developed and the yolks were

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light orange in color. The eggs were incubated at 11°C and hatched on 10 June 1974. Larvae were held in static seawater without food and preserved at 0, 3, and 7 d posthatch. From April to July 1988, older larval stages were taken in epibenthic plankton tows in southern British Columbia, using a sled trawl with a 1.5 m × 0.8 m mouth and 1 mm mesh. The larvae were killed in the cod end bucket with anaesthetic and fixed in 5% formosaline. Several of the largest larvae were removed live and transported to a 1,000 L laboratory tank with through-flowing seawater of 10°C, where they were fed *Artemia* nauplii. Two individuals survived past settlement and were preserved as juveniles.

Unidentified eggs, later found to be *L. callyodon*, were collected from among barnacles and rock crevices in the intertidal zone (0.6 m above low water, Canadian scale) outside Sooke Basin in the Strait of Juan de Fuca (48°20′N, 123°44′W) on 22 March 1987 and 13 March 1988. In 1987, egg masses and newly hatched larvae were directly preserved. A variety of egg masses taken in 1988, ranging in color from maroon to orange to green, were incubated in inflow water of a 1,000 L through-flowing seawater tank and hatches occurred from late March through mid-April from the different masses. Larvae were fed *Artemia* nauplii that had been fed supplemental omega-3 fatty acids (Cooper 1988). Larvae were preserved from the rearing tank at various intervals up to the benthic juvenile stage.

Positive identification of laboratory-reared juveniles was based on the full spectrum of external juvenile characters from the literature (e.g., Hart 1973); larval characters alone could not be used to positively identify to the species level. Median fin ray meristics of late larval stages for these two species overlapped too broadly to permit positive identification prior to the juvenile stage. Juveniles used for identification of both species were deposited in the British Columbia Provincial Museum (BCPM 988-945, BCPM 988-946, BCPM 988-947, BCPM 988-948, BCPM 988-949).

Eggs and larval morphometrics were taken with vernier dial calipers under a dissecting microscope. Upon sorting, measures of notochord length (NL) or standard length (SL) were taken from fixed specimens. Body depth was measured near the pectoral base, where the maximum body depth dimension occurred, including subdermal space (i.e., dorsal epidermis to ventral epidermis). Body length was measured from tip of snout to posterior margin of anus, not including any portion of the abdominal cavity posterior to the anus. Pelvic disk width, not length, was measured. Too few specimens were available to permit clearing and staining, although quick-staining with alizarin red permitted viewing of external features. Illustrations were drawn using a dissecting microscope and camera lucida. Specimens of newly hatched *L. fucensis* from 1974, together with the photographs, permitted redrawing of an illustration from Marliave (1975).

Larvae of *Liparis fucensis*

Pigment intensity varied between siblings hatched in 1974. Similarly, larvae of like sizes and stage, which were captured from the field in 1988, varied in pigment intensity. The overall pattern did not vary much, although a few of the more intensely pigmented individuals tended to prematurely develop sets of melanophores that average larvae develop later. Also, these few intensely pigmented individuals developed a broader extent of particular pigment patches and more numerous, regularly spaced melanophores in rows along the anal fin base and ventral fin fold. Postflexion stages, in particular, tended to show a variation in extent or absence of pigment. Loss of early melanophores and appearances of different sets of melanophores seemed to characterize the postflexion period of development. Overall, however, pigment corresponded clearly to the distribution patterns and intensities illustrated in Figures 1 and 2.

At all stages, the epidermis had a noticeably granular appearance (Fig. 1), except around the outer margins of the tail fin fold. The final development of the expanded subdermal space, or bubble, corresponded to the extent of this granular appearance. On the largest preflexion larva, this granular layer could be scraped away from a basement membrane, on which melanophores remained.

Hatching occurred at 2.9 mm NL; the larvae had a prominent yolk sac with a single anterior oil droplet (Fig. 2a). At hatching, dorsal gut melanophores, about 20 postanal ventral midline melanophores, and a hexagonal honeycomb pattern of melanin on the pectoral fin bases were evident. At 10°C, yolk resorption occurred over a period of seven days under starvation conditions. During that time, larvae grew to 3.3 mm NL; head length increased from 19 to 21.5%

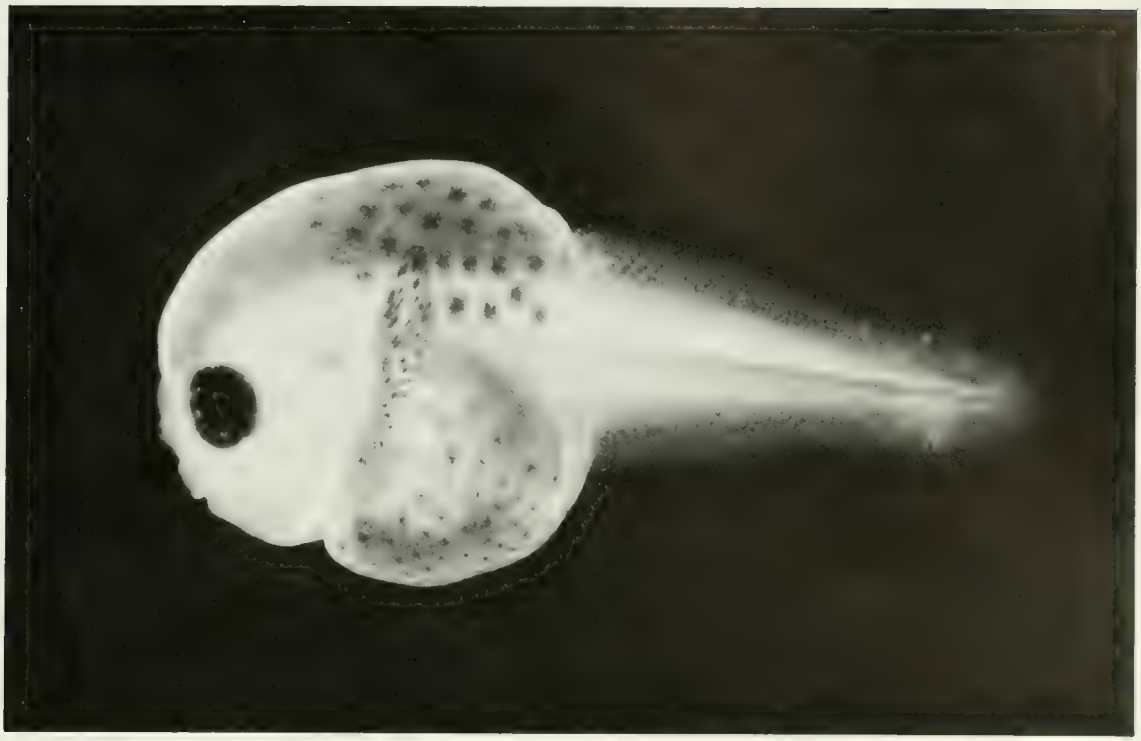

FIGURE 1.—Larva of *Liparis fucensis*, 6.9 mm NL preflexion. Note the granular appearance of the epidermis, visible especially in the cranial region, and the bubble shape of the expanded subdermal space.

NL, while snout-anus length remained at 38% NL. Body depth at yolk resorption was 27.6% NL, and the subdermal space had become prominent in the cranial area by this time. Pigment development during yolk resorption included the appearance of mandibular, ventral gut, and nape melanin, as well as a row of about 10 melanophores on the ventral margin of the fin fold. At hatching, the pectoral fin was only slightly larger than the eye; whereas, by yolk resorption it was 1.7 times as long and 2.3 times higher than the eye. It remained approximately this relative size through the remaining larval stages.

Through preflexion, relative head size increased largely through an increase in the bubble of the subdermal space. This bubble spread from the head region to include the nape and gut region. At 4.1 mm NL, snout-anus length had increased to 44% NL and body depth to 36% NL (Fig. 2b). The overall bubble appearance imparted by the subdermal space (see Figure 1) was evident by this stage, with the posterior margin of the bubble at the anus. Morphometric data on relative body depth and snout-anus length indicated that the development of the bubble is associated particularly with flexion (6–8 mm SL), the period of skeletal development. Just after flexion, a step-function increase in body depth and snout-anus length, relative to head length and standard length, marked the most rapid expansion of this bubble. Nostrils were prominently separated into dorsal and ventral nares by this stage. Through preflexion, pigment remained essentially the same as at the end of yolk resorption. Some preflexion larvae had up to 22 well-spaced, ventral, fin fold melanophores, and up to 24 postanal, ventral, midline melanophores. Such individuals also had denser mandibular melanophores, a few melanophores on the maxillary tip, and a few dorsal, midline melanophores posterior to the nape. Toward the end of preflexion, at 5.25 mm NL, the relative body depth had increased to 42%, and the snout-anus length, to 45%, giving the anterior body a nearly spherical bubble shape. At this size the position of the anus had become anterior to the posterior margin of the bubble portion of the subdermal space by two myomeres. The pelvic disk is not evident in preflexion larvae.

Late during the preflexion stage, larvae between 6 and 7 mm NL started forming dorsal and anal fin rays. These median rays started

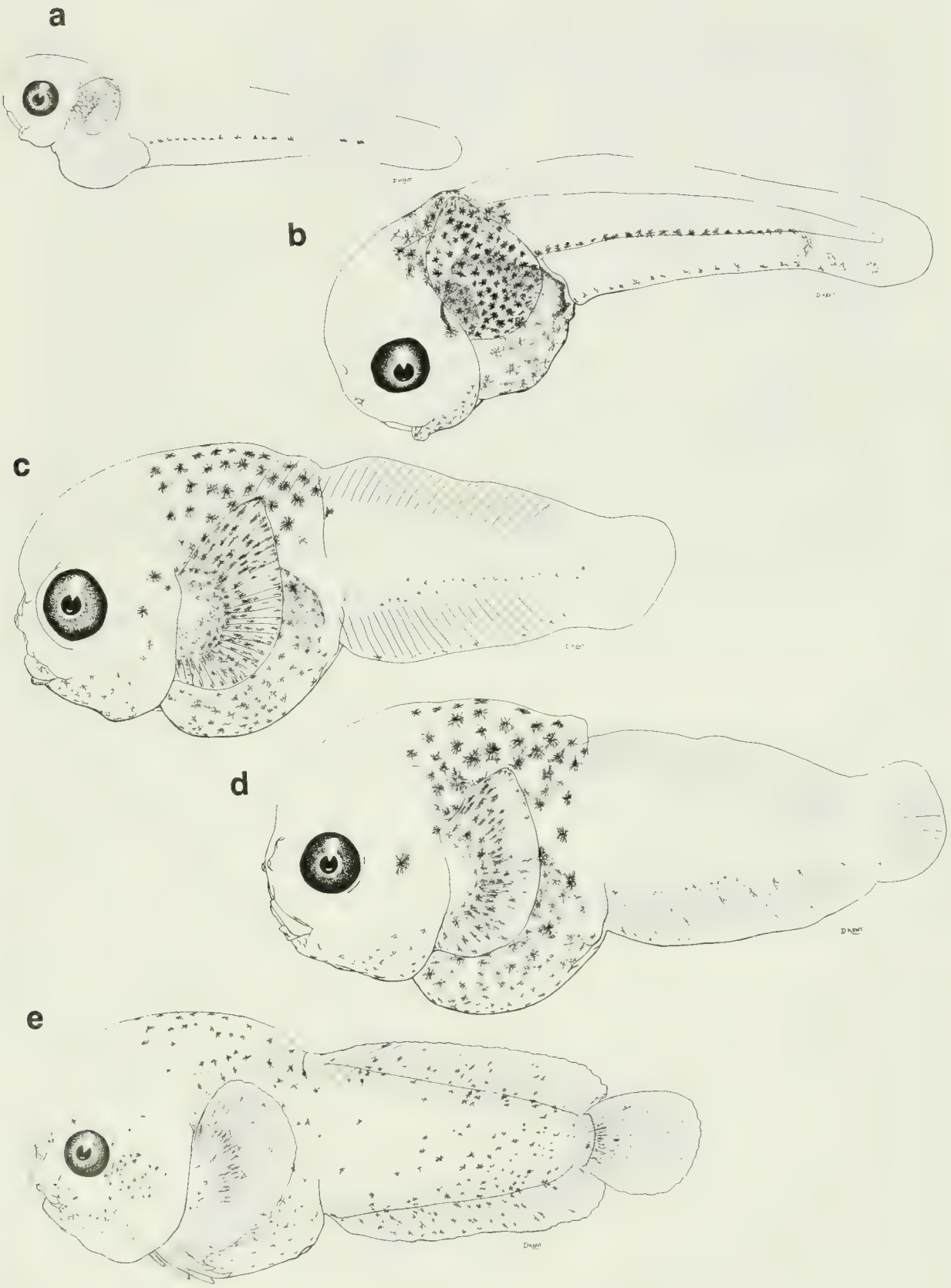

FIGURE 2.—Larvae of *Liparis fucensis*: a, 2.9 mm NL yolksac stage; b, 4.1 mm NL preflexion; c, 6.7 mm NL flexion; d, 8.7 mm SL postflexion; and e, 17.4 mm SL postflexion.

forming anteriorly, extending in decreasing length posteriorly. Pectoral rays were not evident in unstained material. Although the pectorals were very fully pigmented at this stage, the melanophores did not align with the underlying rays.

At the beginning of flexion, larvae between 6.7 and 7.3 mm NL developed dorsal, anal, and pectoral fin rays synchronously, prior to formation of caudal rays (Fig. 2c). Nape, gut, mandibular, and pectoral melanophores remained very prominent, with the addition of a few large melanophores in the opercular area. By this stage, the bubble was large and rather spherical, thus allowing epidermal melanophores to be distinguished readily from gut melanophores. The dorsal bubble melanophores around the nape were large and usually separated by a gap in epidermal pigment laterally, located in the plane of the large dorsal gut melanophores. The ventral bubble melanophores were markedly smaller by this stage, as were the mandibular melanophores. During flexion, postanal ventral, midline melanophores, particularly those in posterior positions, began migrating dorsally along the myosepta. Ventral fin fold melanophores eventually became aligned with the tips of anal fin rays.

During flexion, the final orientation of nares was attained, with the ventral naris on each side oriented anteriorly, and the dorsal naris, dorsally, and with the separation distance between the two nares of each pair similar to that of later stages, i.e., about 0.5 of eye diameter, slightly less than during preflexion. The pelvic disk was well developed and circular at this stage, slightly less than half of eye diameter in size. The pectoral fin did not extend ventrally to the pelvic disk, and no exserted lower rays were present.

During early postflexion, larvae up to 10 mm SL developed lower exserted pectoral rays but only in individuals in which caudal ray formation was completed (Fig. 2d). Early during postflexion, very small, mandibular, acousticolateralis pores became evident, three on each side. The pelvic disk was still small, embedded within an invagination of the bubble. The tail region formed a subdermal swelling, starting anteriorly, at sizes between 9 and 10 mm SL, extending out to under half the length of median fin rays.

Postflexion larvae tended to lose melanophores characteristic at earlier stages, while simultaneously developing new melanophores in other positions. Greater pigment variability between individuals was more evident at this stage than in earlier stages. All postflexion larvae lost the melanophores on the outer half of the pectoral fins, retaining rows of melanophores lining pectoral rays toward the fin base. A few individuals retained very small melanophores lining the fringe of the pectorals. These melanophores were frequently just on the dorsal tip of the pectoral fins, which tended to become less pointed via allometric reduction in ray length when the lower exserted rays formed. The exserted pectoral rays never developed pigmentation in larvae. Many individuals lost the small melanophores on the ventral bubble and mandibles, while the internal melanophores on the gut surface became obscured by the increasing thickness of the granular epidermis (cf. Fig. 1). Melanophores tended to develop along the margin of the tail swelling of the subdermal space, aligned with the midpoints of the dorsal and anal fin rays. At 16.8 mm SL (17.4 mm SL fresh, Fig. 2e), the outer skin was sparsely overlaid with melanophores everywhere except in the anterior cranial area. The melanin was most dense over the preopercular region and between the eye and the maxillary.

The largest postflexion larva, prior to the metamorphic allometry that yielded the juvenile morph, had tubular dorsal nares like the juveniles, but embedded in the bubble. The exserted, ventral, pectoral rays were the same length as the longest pectoral rays dorsally. The anterior portion of the dorsal fin was no longer visible within the bubble. Thus, only 25 posterior dorsal rays and 23 anal rays were evident. The mandibular, acoustico-lateralis pores were prominent and were aligned in a series of four on each side, extending toward the preoperculum. Two smaller pores were over the maxillary on each side. The pelvic disk had developed muscular papillae inside the margin; the shape was a flattened oval, with a width equal to the eye diameter.

The two larvae that survived to the juvenile stage in captivity underwent a metamorphic loss of the subdermal bubble. Over a period of nearly a month in the laboratory, the larvae were observed to show ambivalence between settlement and swimming in the water column. The pelvic disk was functional. Abruptly, the bubble appearance was lost on one juvenile that was observed at that stage; shrinkage occurred, giving the juvenile a slender, distinctively liparidine appearance. The other juvenile could not be

sighted until a later date when growth and deposition of intense dark pigment had occurred. Growth of the juveniles was very rapid compared with *L. callyodon*, as evident in Figure 2 versus Figure 3.

Larvae of *Liparis callyodon*

Preserved egg masses of *L. callyodon* numbered 409, 394, 203, 132, and 53 eggs (egg diameter 1.69 ± 0.02 mm, n = 10). Newly hatched *L. callyodon* averaged 5.21 ± 0.19 mm NL (n = 10). At hatching, snout-anus length averaged 39% NL (2.02 ± 0.16 mm); head length, 21% NL (1.08 ± 0.13 mm); body depth, 22.6% NL (1.18 ± 0.06 mm); and eye diameter, 9.5% NL (0.49 ± 0.02 mm). Pigment at hatching remained the same as in later preflexion stages (Fig. 3a) and consisted of large melanophores covering the entire body, except the posterior end of the notochord. There was also a row of elongated melanophores lining the ventral margin of the fin fold. At hatching, there was no pelvic disk, although the pectoral fin base extended ventrally toward the isthmus where the disk would form. The yolk included a single oil droplet, positioned anterodorsally within the yolk.

Considerable growth in size occurred during preflexion without any visible alteration in appearance (n = 17 specimens). Larvae less than 8 mm NL resembled the 5 mm yolk-sac larvae (Fig. 3). Pelvic disk width was about ⅓ eye diameter. At about 8 mm NL, growth in body depth occurred together with dorsal and anal fin ray formation; the rays formed synchronously along the entire fin lengths. In most specimens, dorsal and anal fin ray formation preceded both caudal and pectoral fin ray formation (Fig. 3b). Disk diameter was about ½ eye diameter at this stage. A few small melanophores had appeared in the dorsal fin area. The hypural primordia were present with no sign of notochord flexion. At lengths between 7 and 8 mm NL, morphometrics remained similar to those at hatching; the greatest changes were an insignificant increase in snout-anus length from 39 to 42% NL and a reduction in body depth from 22 to 19.5% NL.

Just beyond 8 mm NL, hypural plates formed at about the same time as pectoral fin ray bases. However, in a few specimens, these events just preceded anlagen of dorsal and anal fin rays, so the timing of these sets of events was very close and not entirely regular between individuals. At

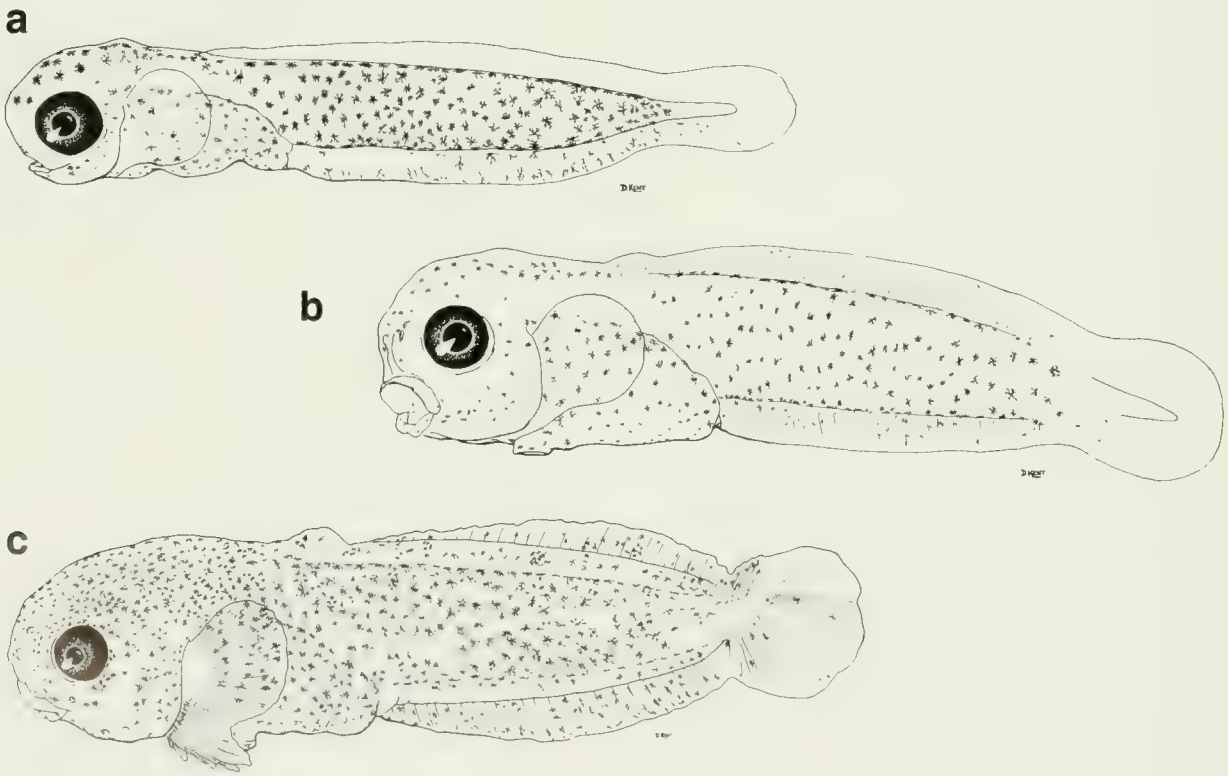

FIGURE 3.—Larvae of *Liparis callyodon*: a, 7.75 mm NL preflexion; b, 8.1 mm NL preflexion; and c, 10.45 mm SL postflexion.

a size of 8.8 mm NL, the hypurals were formed without caudal ray anlagen, and the pectoral fin ray bases were present. The anterior lobe of the dorsal fin (first dorsal) was becoming evident. The pelvic disk was only slightly smaller in diameter than the eye. At sizes between 9 and 9.9 mm NL, caudal rays formed, numbering 8 or 10 in different specimens, and pectoral rays developed from ½ to over ¾ of their length. All larvae under 10 mm NL were preflexion larvae. Larvae between 8.8 and 9.9 mm NL had the same morphometrics as smaller preflexion larvae, except a reduction from 9 to 7% NL in eye diameter.

Flexion occurred at sizes just beyond 10 mm NL, together with completion of caudal and pectoral fin ray formation. At 10.45 mm NL, the exserted lower pectoral rays were elongated, and the anterior lobe of the dorsal fin was becoming prominent. Disk width equalled eye width. Caudal pigment was forming, and the melanin on the rest of the body had become denser, although the pectoral fin remained unpigmented. The mandibular area was lined with 10 acoustico-lateralis pores (5 each side), and the maxillary region, with 8 pores. The nostrils were split into separate canals, with the ventral naris directed anteriorly in line with the eye pupil (about 66% pupil diameter) and with the dorsal naris directed up at a 45° angle to the level of the notochord (the opening half the diameter of the ventral naris). The cranial subdermal space was evident beneath the dense melanin. The operculum remained entirely open along the pectoral fin base and did not extend dorsally beyond the pectoral fin.

During postflexion (Fig. 3c), ambivalence between swimming and settlement became evident in the rearing tank (n = 3 individuals). Postflexion juveniles of about 12 mm NL had formed an acoustico-lateralis pore posterior to the eye, and two pores of the lateral line, immediately posterior to the dorsal end of the operculum. The operculum extended dorsally beyond the pectoral base, curving anteriorly as in adults. The opercular membranes with branchiostegals were fused with the isthmus up to about 7 rays from the top of the pectoral fin.

Juveniles of 20–22 mm SL showed different morphometrics from larvae: the snout-anus length was reduced from 42 to 36% SL; the eye diameter was further reduced to 5.7% SL; the head length increased from 21 to 24.4% SL; and the body depth slightly increased to 23.5% SL. In permanently settled juveniles at the largest sizes preserved, the opercular opening remained as low as the 4th or 5th pectoral ray; whereas, adult *L. callyodon* would not have this opening extending beyond the 1st ray (Hart 1973). The only other possible identifications from meristics were *L. cyclopus* and *L. florae*, but morphometrics, fin shape, and ecological information dictated against such determinations.

DISCUSSION

It must be reiterated that positive identification was, and now remains, possible only from juvenile material reared from known larvae. Future work may possibly permit identification from larval material for these Pacific *Liparis* species, but the present work serves only to focus such future efforts.

Taxonomic identification of *Liparis* species depends on numerous characters that are very difficult to determine in the smallest juvenile specimens. In addition, the opercular opening becomes smaller with development in *Liparis* species (Able et al. 1984). Therefore, rigid adherance to determining a restricted opercular opening size for identification of *L. callyodon* (cf. Hart 1973) should be expected to cause difficulty in identification of small juveniles. Further investigation of allometric reduction in opercular opening size in juveniles of the genus *Liparis* is required.

The fecundity (fewer than 400 eggs per mass) of *L. callyodon* was substantially less than the fecundity (about 1,500 to 5,000 eggs) determined for *L. fucensis* by DeMartini (1978). The average egg size, however, was larger at 1.7 mm for *L. callyodon* than for *L. fucensis* at 1 mm (Marliave 1975; DeMartini 1978). Adults of *L. fucensis* attain 30% greater maximum length than *L. callyodon* (Hart 1973). Furthermore, the *L. callyodon* egg masses collected, especially the counts of 132 and 53, may not have comprised the entire ovarian output of a female in every case because eggs were extruded into available interstitial spaces. This could sometimes restrict the number of eggs laid in one mass.

The larger eggs and apparent lower fecundity of *L. callyodon* resulted in considerably larger larvae at hatching than those for *L. fucensis*. Growth and development of *L. callyodon* occurred over a smaller range of lengths. Considering the cubic increase in volume with length for the bubblemorph of *L. fucensis* larvae, that unusual morph permitted enormous growth during the larval stage compared to the more typical *Liparis* larvalmorph of *L. callyodon*. Larvae of

L. callyodon resemble the few Atlantic species of *Liparis* that have been identified (Able et al. 1984), except for the unusually heavy melanization in larvae of this species. Intense melanization at hatching is more typical of cyclopterine than liparidine larvae (Able et al. 1984).

Although a relatively large subdermal space surrounding the entire body is typical of liparidine larvae, it is only as prominent as that illustrated in Figure 1 in *L. fucensis*, which may be the same species as that unidentified illustration previously referred to (by Able et al. 1984). That previously published illustration shows development of fin rays at a smaller size and with less melanin than in the present paper, but both of these features could result from the shrinkage and bleaching effects of long-term preservation. Another explanation for such differences is that regional differences might occur, as described for larvae of another cottoid species, *Oligocottus maculosus* (Marliave 1988). On the other hand, the unidentified illustration of a liparidine bubblemorph was drawn from a CalCOFI sample, which would be just south of the known range for *L. fucensis* (Hart 1973).

The larval bubblemorph of *L. fucensis* was collected in sled trawl tows taken within 1 m of the bottom at a wide variety of depths. In these same tows, larvae of Pacific whiting, *Merluccius productus*, were caught in the bottom tows at stages in which their swimbladder had developed, whereas earlier stages tended to be uniformly distributed through the water column (Marliave in press). Since cottoid fishes lack swimbladders at all stages, the evolution of a larval bubblemorph in the cyclopterid *L. fucensis*, in the cottid *Malacocottus zonurus* (Washington et al. 1984), and, to a less obvious extent, in the cottids *Gilbertidia sigalutes* and *Psychrolutes paradoxus* (Marliave 1975) may be an adaptation imparting neutral bouyancy, which would assist in maintaining a precise depth without costly swimming effort. The fluid of the subdermal space, if maintained at bodily osmolarity well below that of ambient seawater, would reduce overall density and lend to neutral bouyancy. Larvae possess swimbladders in certain other taxa that lack a swimbladder as benthic adults, as in the Gobiesociformes (Allen 1984); thus, the selective advantage of achieving neutral bouyancy appears to be relatively general among larval marine fishes.

Convergence toward the bubblemorph and midwater habitat is found in other genera. Most notably, Peden and Anderson (1978, 1979), Anderson (1977), and Peden (1979) discussed either the loose skin, which imparts a sort of bubble morphology, or the midwater habitat (i.e., neutral buoyancy) of the zoarcid genus *Lycodapus*. Anderson (1977, 1984) further noted that same habitat in *Melanostigma*, although this genus may possibly deposit demersal eggs in one species, *M. atlanticum*. Among liparidines, midwater habitat and bubble morphology are most specialized in *Nectoliparis* and *Lipariscus*; these genera retain this specialized larval character into adult life (see Peden 1981 regarding midwater habitat). In these four genera, representing two distinctly divergent families with demersal ancestors, eggs producing relatively large and well-developed young are apparently deposited and reared, for most species, in the same midwater habitat as adults. In the case of the better known *Lycodapus mandibularis* (Anderson 1977; Peden and Anderson 1978; Peden 1979), adults are not known to select bottom habitat except accidentally during diel migration (Peden observation from submersible). Young, as small as 19 mm, are found in the same midwater tows as adults (maturity is at 75–90 mm in northern samples); owing to the large size of the eggs (Anderson 1977), the young are assumed to have hatched at relatively large sizes. Given the development of loose skin, or bubble morphology, in the more specialized and diverse genera of liparidines *Careproctus* and *Paraliparis* (Burke 1930; Stein 1978), many of which are from midwater, the bubblemorph, which originally evolved in a *Liparis*-like ancestor, has apparently been exploited in adult life histories of a large number of species. In some of these liparidine and zoarcid genera, some species may be associated with near-bottom habitats, and the bubblemorph may allow adults to hover just off the bottom similar to fishes with swimbladders (observed in *Lycodapus parviceps* by Peden from submersible).

The relatively neutral bouyancy that seems probable for the cottoid bubblemorph might permit relatively greater overall growth during the planktonic stage than for larvae of related species that have more typical larval morphology; e.g., larval *Gilbertidia sigalutes* grow to about 75% of their average adult size during the planktonic stage (Marliave 1981). This difference in larval growth seems to be the case for the present two *Liparis* species; the normal-type *L. callyodon* settles from the plankton at a very small size compared with the bubblemorph of *L. fucensis*. Bouyancy and potential growth rate

are both features that should be under immediate selective pressure; thus the presence or absence of the bubble morphology would be a derived character not suitable for revealing phylogenetic relationships.

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Development and Distribution of Larvae and Pelagic Juveniles of Three Kyphosid Fishes (*Girella nigricans*, *Medialuna californiensis*, and *Hermosilla azurea*) off California and Baja California

Elizabeth G. Stevens, William Watson, and H. Geoffrey Moser

ABSTRACT: Complete developmental series are described for larvae and pelagic juveniles of three kyphosid fishes, *Girella nigricans* (Ayres), *Medialuna californiensis* (Steindachner), and *Hermosilla azurea* (Jenkins and Evermann), from California and Baja California coastal waters. Larvae of the three species have a similar compact body form, with *G. nigricans* being the most slender and *H. azurea* the most robust. They share a number of pigment characters: including dorsal, ventral, and lateral midline melanophore series; an embedded melanistic band through the eye region; and minute melanophores at the tip of the notochord. Unique pigment variations permit the identification of all developmental stages of these species. Each has a specialized pelagic juvenile stage with distinct pigmentation. The pelagic distribution of each species is described; larvae of *M. californiensis* are the most oceanic and those of *H. azurea* the most coastal of the three species. The ontogenetic characters of these species are consistent with the view that they are monophyletic.

The opaleye, *Girella nigricans*, occurs from San Francisco, California, to Cabo San Lucas, Baja California. It is a prominent member of nearshore rocky reef and kelp communities from southern California to central Baja California and ranges from the intertidal zone to about 30 m depth. The halfmoon, *Medialuna californiensis*, occurs from Vancouver Island, Canada, to the Gulf of California, but is rare north of Point Conception, California. Its preferred habitat is similar to that of *G. nigricans*, although it ranges deeper to 40 m. The zebra perch, *Hermosilla azurea*, is known from Monterey Bay, California, to the Gulf of California but prefers warmer waters and is rare north of southern California. It is found in shallow inshore areas to a maximum depth of 8 m (Miller and Lea 1972; Feder et al. 1974; Eschmeyer et al. 1983).

Opaleye and halfmoon are part of the incidental catch of the coastal purse seine fleet and are sold as "perch" in the fresh fish market (Fitch and Lavenberg 1971). Annual landings of opaleye average about 2½ tons with a maximum of 12 tons in 1973; halfmoon landings average about 7 tons annually with a maximum of 25 tons in 1968 (Heimann and Carlisle 1970; McAllister 1975). Halfmoon are seasonally abundant in the southern California commercial passenger fishing boat catch, ranking as high as fifth in numbers caught (Crook 1978). They also consistently rank among the top 10 species caught by the southern California private sport fishery (Wine 1982). Fewer opaleye are landed in these fisheries, reflecting the shallower distribution of this species; however, opaleye are a mainstay for rocky-shore anglers in southern California and are the second most important species in competitive spearfishing events (Pinkas et al. 1968; Fitch and Lavenberg 1971). Zebra perch are taken occasionally by southern California shore anglers and spearfishers (Limbaugh 1955; Feder et al. 1974).

Knowledge of the early life histories of opaleye and halfmoon is scanty. They spawn during spring and summer and their larvae appear in nearshore plankton tows during this period. Both species have a silvery pelagic juvenile stage, and both appear in small schools in nearshore areas and around floating masses of kelp. Halfmoon continue their juvenile development in these habitats, whereas opaleye enter tidepools at about 25 mm length and change abruptly to olive colored individuals which have one or two white spots on the back, lateral to the dorsal fin. They remain in the intertidal region until about

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75 mm length when they begin to seek deeper subtidal habitats (Limbaugh 1955; Fitch and Lavenberg 1971; Kramer and Smith 1973; Feder et al. 1974; Gruber et al. 1982; Walker et al. 1987; Waples 1987; Waples and Rosenblatt 1987). Information on zebra perch is limited; their larvae occur in nearshore plankton tows in summer and fall (Walker et al. 1987) and small juveniles are reported to school with those of opaleye in August (Lockley 1952; Limbaugh 1955; Feder et al. 1974).

The systematic placement of these species is unsettled. Hubbs et al. (1979) and earlier workers recognized separate families for each of them, placing *G. nigricans* in Girellidae, *M. californiensis* in Scorpididae, and *H. azurea* in Kyphosidae; other workers have grouped the three species in Kyphosidae (Robins et al. 1980). Johnson (1984) maintained separate families for these species in his survey of percoid ontogeny and included two of our original drawings (10.9 mm *G. nigricans* and 10.1 mm *M. californiensis*) in his review.

The purpose of this paper is to describe the larvae and pelagic juveniles of *G. nigricans*, *M. californiensis*, and *H. azurea*, summarize their distributions from California Cooperative Oceanic Fisheries Investigations (CalCOFI) surveys and other sources, and point out ontogenetic characters that may be useful in defining systematic relationships.

MATERIALS AND METHODS

Larvae and pelagic juveniles of *G. nigricans* and *M. californiensis* were obtained principally from CalCOFI plankton surveys, while those of *H. azurea* came from nearshore plankton samples off the San Onofre Nuclear Generating Station (SONGS) (Barnett et al. 1984). Totals of 213 larvae and 111 pelagic juveniles were available for *G. nigricans*; 253 larvae and 31 pelagic juveniles for *M. californiensis*; and 79 larvae and 6 pelagic juveniles for *H. azurea*. Additional larval specimens of *G. nigricans* were obtained from a batch of field-caught eggs reared by David Kramer in the experimental aquarium of the Southwest Fisheries Center from 1 to 28 June 1968. We reared several batches of *G. nigricans* larvae from field collections of eggs in May to July 1978 and in July 1979. None of these larvae survived more than one week; however, they were useful in defining early pigment patterns.

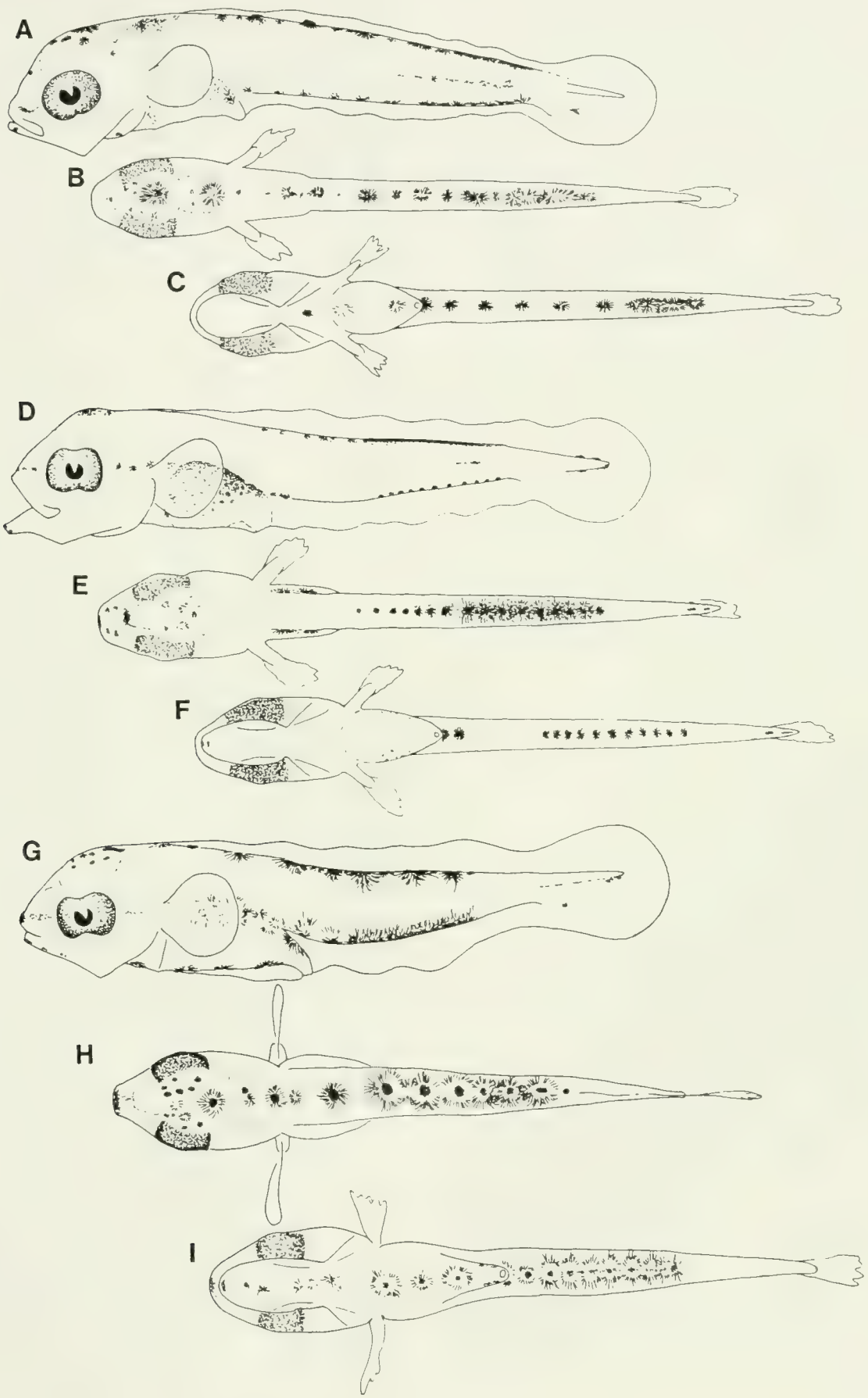
Developmental series were established to study general morphology, morphometry, and pigmentation; selected specimens were cleared and stained using the method of Potthoff (1984) to determine the sequence of ossification of fin rays, vertebrae, branchiostegal rays, and head spines. The descriptive methods and terminology follow Ahlstrom et al. (1976) and Johnson (1984). Prior to the completion of notochord flexion, body length was measured from the tip of the snout to the tip of the notochord and is designated notochord length (NL). In postflexion specimens body length was measured to the posterior edge of the hypural plate and is termed standard length (SL).

DISTINGUISHING FEATURES OF THE SPECIES

Larvae of the three species can be separated by melanistic pigment pattern (Fig. 1). Preflexion and flexion stage larvae of *G. nigricans* have one or two melanophores on the ventral midline of the gut. *Hermosilla azurea* usually have 3 or 4 (range, 1–6) evenly spaced melanophores in this region and *M. californiensis* larvae lack ventral gut melanophores during these stages. Preflexion and flexion larvae of *G. nigricans* and *H. azurea* have a series of evenly spaced melanophores along the ventral margin of the tail usually beginning at the first postanal myomere; in *M. californiensis* the series often is incomplete anteriorly (except in yolk-sac larvae). Larvae of *M. californiensis* usually have small melanophores dorsally and ventrally near the tip of the notochord. These melanophores are smaller, fewer, and often present only on the ventral margin in the other two species.

All three species are heavily pigmented along the dorsal and ventral margins through most of larval life and all three acquire a midlateral streak along the tail during notochord flexion. The streak originates more posteriorly in *M. californiensis* than in the other two species. In flexion larvae of *M. californiensis* and *H. azurea*, pigment spreads from the dorsal, lateral, and ventral series to form a band around the tail. This band originates more anteriorly

FIGURE 1.—Lateral, dorsal, and ventral views of early kyphosid larvae: (A–C) *Girella nigricans*, 5.7 mm NL, CalCOFI cruise 7805, station 90.28, surface tow; (D–F) *Medialuna californiensis*, 5.2 mm NL, CalCOFI cruise 6207–B, station 110.55, oblique tow; (G–I) *Hermosilla azurea*, 4.3 mm NL, MEC SONGS cruise I–80, surface tow.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and is broader in the latter species, although in both species it subsequently expands anteriorly to completely cover the sides of the body. Late larvae and pelagic juveniles of all three species are heavily pigmented; *G. nigricans* maintains a strong midlateral stripe, *M. californiensis* becomes uniformly pigmented, and *H. azurea* develops a mottled or barred pattern.

The three species differ in body depth, with *G. nigricans* the most slender and *H. azurea* the most robust. Developmental events occur at a smaller size in *H. azurea* than in the other species. Notochord flexion occurs between 4.1 and 5.8 mm in *H. azurea*, and between 5.8 and 8.6 mm in *G. nigricans* and *M. californiensis*. Transformation to pelagic juveniles occurs at about 11–12 mm in *H. azurea*, ca. 17 mm in *G. nigricans* and ca. 12 mm in *M. californiensis*. Head spination is more developed in *M. californiensis* than in the other two species.

Dorsal and anal fin ray counts are distinct for all three species at about 10 mm SL. *Hermosilla azurea* has XI, 11 dorsal rays and III, 10 anal rays while these fin formulas are D: XII–XIV, 12–15, A: III, 10–13 for *G. nigricans* and D: IX–X, 22–27, A: III, 17–21 for *M. californiensis* (Miller and Lea 1972).

Girella nigricans

Figures 1–3

General Morphology

Our smallest yolk-sac larvae are ca. 3.0 mm, have unpigmented eyes, a rudimentary mouth, and a large oval yolk sac which extends from the head to ca. midintestine and contains a single posteriorly located oil globule (ca. 0.16–0.20 mm diameter). Larvae are 3.5–3.7 mm long when the yolk is completely absorbed. Preflexion larvae are moderately slender with a relatively short coiled gut which extends slightly less than 40% of body length (Tables 1, 2). A small gas bladder is positioned anteriorly above the gut. The head is relatively small, with a blunt snout, and with round to slightly elongate (horizontally) eyes (Fig. 2).

Development is gradual during flexion and postflexion with no abrupt changes in body form or proportions. Most body parts increase relative to body length throughout the larval period with snout-anus length, head length, and body depth showing the greatest changes (Table 2). A small blunt spine develops at the angle of the preopercle in late preflexion larvae, and remains inconspicuous during later larval stages. No other head spines develop in larvae; however, one or more additional minute preopercular spines may appear in early pelagic juveniles. These specimens also develop an opercular and a minute supracleithral spine.

Notochord flexion begins at ca. 5.8 mm length and is completed by ca. 8.6 mm. Transformation into the pelagic juvenile stage is indicated by the appearance of scales (first seen in a 15.7 mm specimen), completion of fin ray elements, and attainment of juvenile pigment at about 17 mm (Fig. 3).

Fin Formation and Meristics

The first rays to calcify are the central principal caudal rays beginning late in the preflexion stage at ca. 5.8 mm (Table 3). The full complement of 9+8 principal rays is present midway through flexion and the procurrent rays begin to calcify at the end of flexion. The full complement of 10–12+9–10 procurrent rays is acquired in early pelagic juveniles (Table 3).

The dorsal and anal soft rays begin to calcify during flexion. Addition is posteriad with full complements attained in early postflexion. Dorsal and anal spines appear during early postflexion and are added in an anteriad direction. Full dorsal and anal fin complements (D: XII–XIV, 12–15; A: III, 10–13) are present in postflexion larvae 10.7 mm and larger.

The pectoral fins are initially rounded with rounded bases and retain this shape throughout the larval period; they become more elongate in pelagic juveniles. Calcification of rays begins midway through flexion; the upper rays are the first to appear and addition is ventrad. The full complement of 18–20 is present just before transformation into the pelagic juvenile.

The pelvic fins are the last to form. Fin buds appear midway through flexion and calcification of rays begins just after flexion is completed. The full complement of I,5 rays was present in specimens 10.7 mm and larger.

Initial vertebral ossification was not apparent in our stained series; however, the anteriormost 22 vertebral centra were already ossifying in a 6.7 mm larva. Ossification proceeds in a posteriad direction and the full complement of 27 vertebrae is present by the end of flexion. The branchiostegal rays begin to ossify late in preflexion and the full complement of six pairs of rays is present late in flexion.

TABLE 1.—Measurements (mm) of larvae and pelagic juveniles of *Girella nigricans*. Broken lines enclose specimens undergoing notochord flexion and specimens below solid line are pelagic juveniles.

Station	Body length	Snout-anus length	Head length	Head depth	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Predorsal length	Prepelvic length
6606–93.27	2.6	0.96	0.54	0.60	0.10	0.34	0.54	—	—	—	—
6307–83.39	2.7	0.86	0.51	0.44	0.08	0.28	0.46	0.14	—	—	—
8105–83.3.42	2.8	1.1	0.56	0.58	0.08	0.24	0.46	0.20	0.10	—	—
6606–93.27	2.9	1.2	0.65	0.74	0.09	0.22	0.60	0.20	0.10	—	—
8105–83.3.42	3.0	1.1	0.62	0.58	0.14	0.20	0.50	0.22	0.11	—	—
8105–83.3.42	3.1	1.1	0.64	0.64	0.16	0.20	0.56	0.30	—	—	—
6606–93.27	3.2	1.2	0.74	0.70	0.16	0.32	0.60	0.30	0.14	—	—
6509–120.40	3.4	1.4	0.45	0.48	0.11	0.26	0.45	—	—	—	—
6110–127.34	3.5	1.2	0.71	0.62	0.11	0.29	0.54	0.30	—	—	—
8105–83.3.42	3.6	1.2	0.72	0.66	0.12	0.26	0.60	—	—	—	—
SCBSIII 303	3.8	1.4	0.78	0.64	0.11	0.30	0.60	0.40	0.18	—	—
5710–123.37	4.1	1.8	1.0	0.80	0.22	0.34	0.79	0.60	0.22	—	—
SCBSIII 303	4.2	1.7	0.88	0.80	0.12	0.36	0.70	0.40	—	—	—
8105–103.3.29	4.3	1.8	1.0	0.80	0.22	0.42	0.78	0.46	0.18	—	—
5607–97.40	4.4	1.6	1.1	0.82	0.18	0.40	0.76	0.32	—	—	—
5708–127.34	4.5	1.8	0.86	0.84	0.23	0.33	0.80	0.44	0.16	—	—
8108–106.7.31	4.7	1.8	1.3	0.94	0.28	0.50	1.0	—	0.24	—	—
6310–87.32.5	4.8	2.0	1.2	0.96	0.24	0.42	0.84	0.60	0.22	—	—
6507–93.26	4.9	1.9	1.1	0.92	0.21	0.41	0.88	0.80	—	—	—
7805–90.28	5.8	2.0	1.4	1.1	0.32	0.52	1.0	0.60	0.36	—	—
5910–127.34	6.0	2.3	1.5	1.3	0.40	0.54	1.2	0.60	0.36	—	—
8107–83.3.42	6.1	2.3	1.5	1.2	0.36	0.56	1.3	0.60	0.34	3.2	—
8105–103.3.29	6.2	2.3	1.6	1.2	0.24	0.60	1.2	0.60	0.42	3.2	1.8
7805–90.28	6.3	2.4	1.5	1.2	0.36	0.60	1.2	0.64	0.36	3.3	—
8105–103.3.29	6.4	2.5	1.7	1.1	0.42	0.56	1.1	0.80	0.36	3.4	—
7805–90.28	6.5	2.3	1.6	1.2	0.32	0.60	1.2	0.88	0.40	3.3	1.5
8107–93.3.50	6.6	2.6	1.4	1.4	0.34	0.66	1.4	1.0	0.50	4.0	2.1
8107–93.3.50	6.7	2.7	1.8	1.5	0.46	0.72	1.5	0.80	0.30	3.7	2.1
7805–90.28	6.8	2.5	1.8	1.3	0.34	0.62	1.3	0.60	0.32	3.8	2.0
7805–90.28	7.0	2.8	1.9	1.4	0.40	0.68	1.4	0.82	0.40	4.0	2.0
7805–90.28	7.1	2.8	2.0	1.4	0.42	0.68	1.4	0.76	0.56	3.9	2.0
8105–103.3.29	8.2	3.6	2.4	1.7	0.48	0.88	1.8	1.1	0.42	3.8	2.7
8107–80.51	8.4	3.8	2.4	1.7	0.40	0.84	1.7	0.92	0.54	4.8	2.5
8105–86.7.35	8.6	3.7	2.5	1.8	0.60	0.88	1.9	1.2	0.56	4.0	2.8
8105–86.7.45	8.6	4.0	2.8	2.1	0.60	0.88	2.2	1.2	0.70	3.8	2.9
8105–86.7.33	10.7	5.5	3.1	2.2	0.64	1.1	2.5	—	0.68	3.9	3.4
7803–90.60	11.9	5.7	3.3	2.0	0.74	1.2	2.5	1.8	0.68	3.8	3.8
8108–96.7.35	14.8	8.1	4.9	3.8	1.0	1.6	3.8	2.6	0.80	5.7	5.2
8107–93.3.55	15.8	8.5	5.0	3.4	1.2	1.5	3.8	3.2	0.92	5.2	5.2
8107–93.3.55	16.5	8.3	5.2	3.7	1.2	1.6	4.1	2.8	1.0	6.0	6.0
8107–80.55	17.3	9.2	5.5	3.7	1.3	1.8	4.2	3.3	1.2	5.8	5.7
8108–103.3.30	18.4	10.3	5.8	4.5	1.5	1.8	5.0	3.4	1.2	6.8	6.7
8102–120.30	19.5	10.8	5.8	4.6	1.4	1.8	5.1	4.8	1.2	6.9	6.4
6612–123.36	23.2	12.0	6.9	5.8	1.8	2.2	6.7	5.0	1.6	8.2	7.7

TABLE 2.—Average body proportions (% ± standard deviation) for larvae of

Species/stage	Snout-anus length / Body length	Head length / Body length	Head depth / Body length	Snout length / Body length	Eye diameter / Body length
Girella nigricans					
Preflexion	38.2 ± 2.92	21.5 ± 3.07	19.3 ± 2.49	4.1 ± 1.06	8.7 ± 1.58
Flexion	38.9 ± 2.91	25.8 ± 2.15	19.8 ± 1.35	5.6 ± 0.82	9.6 ± 0.60
Postflexion	49.6 ± 4.15	30.7 ± 2.05	21.8 ± 2.88	6.8 ± 0.57	10.1 ± 0.42
Juvenile	54.1 ± 1.99	30.7 ± 1.13	23.6 ± 1.57	7.7 ± 0.43	9.7 ± 0.51
Medialuna californiensis					
Preflexion	39.6 ± 2.49	21.2 ± 3.23	19.1 ± 2.09	4.1 ± 1.23	8.4 ± 0.64
Flexion	44.3 ± 4.31	27.2 ± 3.88	21.8 ± 2.21	6.3 ± 0.86	10.7 ± 1.15
Postflexion	50.6 ± 4.13	30.5 ± 3.29	23.3 ± 1.46	6.0 ± 0.75	10.8 ± 0.33
Juvenile	56.5 ± 2.29	33.4 ± 1.75	27.2 ± 2.05	6.7 ± 0.92	10.6 ± 0.70
Hermosilla azurea					
Preflexion	51.0 ± 3.23	28.4 ± 3.10	23.5 ± 3.31	6.1 ± 1.66	11.0 ± 0.47
Flexion	54.2 ± 3.06	31.9 ± 3.90	24.0 ± 3.42	7.9 ± 1.46	11.6 ± 1.06
Postflexion	57.3 ± 1.03	31.7 ± 2.25	25.8 ± 1.72	7.5 ± 0.55	12.2 ± 0.75
Juvenile	58.0 ± 1.83	32.8 ± 1.89	25.8 ± 2.06	6.5 ± 0.58	11.2 ± 0.96

Pigmentation

Pigmentation of yolk sac and early preflexion larvae was described by Orton (1953) from specimens cultured in the laboratory. Newly hatched larvae have a few melanophores on the hindgut and in a short midventral row at the base of the tail. At about midway through yolk absorption, small melanophores appear on the ventral surface of the yolk sac (Fig. 2A); the row above the hindgut becomes heavier, extending forward to about the midpoint of the yolk sac; and the midventral tail series has increased to 7–11 melanophores, extending posteriad along most of the tail. A series of small melanophores appears on the dorsal midline along the posterior half of the tail, and several small melanophores are present above and below the tip of the notochord. Near the end of yolk absorption the eyes become pigmented; the dorsal gut pigment becomes heavier and extends over the entire gut; and the ventral tail melanophores enlarge, partly by aggregation, as do the melanophores on the dorsal margin of the tail.

In early preflexion larvae the ventral midline series of 5–8 large melanophores is continuous with the dorsal gut melanophores. A space separates the ventral tail series from one or more smaller melanophores near the tip of the notochord. The dorsal midline series consists of ca. 1–4 large melanophores posteriorly on the tail, with one to several small melanophores near the tip of the notochord. A large melanophore develops above the midbrain and one forms on the nape. Internal pigment develops below each otic capsule, appearing as a continuation of the dorsal gut pigment. The series of small ventral gut melanophores coalesces into 3 pigment loci, each usually containing a single melanophore: 1) an embedded melanophore anterior to the liver, 2) a surface midventral spot just posterior to the liver, 3) a surface midventral spot just anterior to the hindgut (Fig. 1C).

During preflexion the dorsal gut pigment expands to the lateral surface of the gut. The dorsal midline series increases anteriorly beginning in early preflexion, and soon extends from the head nearly to the tip of the tail. The smaller melanophores near the tip of the tail disappear or are reduced to one. Dorsal melanophores number 11–15. The smaller ventral spots at the notochord tip disappear, except for one, which persists in the finfold about halfway between the end of the ventral pigment series and the tip of the tail.

During late preflexion and flexion stages, pigment increases on the midbrain and appears on both the forebrain and hindbrain. Paired melanophores develop on the roof of the mouth below the nasal capsules and olfactory lobes, and one or more form at the tip of the lower jaw. As the pigment associated with the otic capsule increases, an embedded stripe passing through the eye region is formed (Fig. 2E). One or two surface melanophores appear posterior to the eye in the opercular region. Melanophores appear on the tip of the lower jaw, at the angle of the jaw, and later along the rami of the jaw. A large

Girella nigricans, *Medialuna californiensis*, and *Hermosille azurea*.

Species/stage	Body depth / Body length	Pectoral fin length / Body length	Pectoral fin base depth / Body length	Predorsal length / Body length	Prepelvic length / Body length
Girella nigricans					
Preflexion	17.6 ± 1.98	9.7 ± 3.00	4.3 ± 0.69		
Flexion	19.8 ± 1.58	11.3 ± 1.79	6.0 ± 0.97	54.0 ± 3.69	29.4 ± 2.83
Postflexion	23.8 ± 1.77	16.3 ± 2.42	6.3 ± 0.89	37.7 ± 4.81	33.4 ± 1.68
Juvenile	26.6 ± 1.92	21.0 ± 2.78	6.6 ± 0.34	35.3 ± 1.43	33.8 ± 1.72
Medialuna californiensis					
Preflexion	17.0 ± 2.22	10.2 ± 1.29	4.7 ± 1.44		
Flexion	22.4 ± 2.49	12.2 ± 2.05	6.8 ± 0.83	44.8 ± 6.69	34.5 ± 2.43
Postflexion	24.2 ± 2.23	16.8 ± 3.46	6.6 ± 0.72	42.4 ± 5.80	33.8 ± 2.62
Juvenile	29.3 ± 0.71	22.0 ± 1.53	6.2 ± 0.74	38.1 ± 2.12	38.1 ± 1.13
Hermosilla azurea					
Preflexion	22.5 ± 2.59	12.0 ± 0.82	7.9 ± 1.12		
Flexion	24.5 ± 2.33	12.9 ± 2.23	9.1 ± 0.83	39.4 ± 1.99	36.6 ± 0.40
Postflexion	25.8 ± 1.17	16.4 ± 4.16	7.8 ± 0.98	40.3 ± 2.42	39.3 ± 2.42
Juvenile	31.2 ± 1.50	25.0 ± 2.45	7.2 ± 0.50	40.2 ± 1.26	38.5 ± 1.91

TABLE 3.—Meristics of cleared and stained specimens of *Girella nigricans*. Broken lines enclose specimens undergoing notochord flexion and specimens below solid line are pelagic juveniles.

Length (mm)	Principal caudal fin rays		Procurrent caudal fin rays		Branchiostegal rays		Pectoral fin rays		Dorsal fin rays	Anal fin rays	Pelvic fin rays		Vertebrae
	Superior	Inferior	Superior	Inferior	Left	Right	Left	Right			Left	Right	
5.8	3	3	—	—	3	3	—	—	—	—	—	—	—
6.0	6	6	—	—	4	4	—	—	—	—	—	—	—
6.5	8	7	—	—	5	5	—	—	—	—	—	—	—
6.7	8	7	—	—	5	5	—	—	—	—	—	—	22
7.0	9	8	—	—	5	5	—	—	—	—	—	—	24
7.2	9	8	—	—	6	6	6	6	5	—	—	—	26
7.9	9	8	1	1	6	6	10	10	13	10	—	—	27
8.2	9	8	1	1	6	6	9	10	12	10	1	1	27
9.1	9	8	1	1	6	6	14	14	—	—	I,4	I,4	27
10.7	9	8	5	5	6	6	17	17	XIII,14	III,12	I,5	I,5	27
11.7	9	8	6	5	7	7	17	17	XIII,15	III,11	I,5	I,5	27
12.0	9	8	5	5	6	6	18	18	XIII,13	III,11	I,5	I,5	27
15.7	9	8	10	9	6	6	20	20	XIII,12	III,11	I,5	I,5	27
21.8	9	8	12	9	6	6	19	19	XIV,13	III,11	I,5	I,5	27
22.0	9	8	10	10	6	6	18	19	XV,13	III,11	I,5	I,5	27
37.0	9	8	11	10	6	6	19	19	XIV,13	III,10	I,5	I,5	27

melanophore appears on the isthmus just anterior to the gut, often preceded by a series of several smaller spots. The pigment on the ventral surface of the gut may also increase to form a series of pigment dashes.

At this stage a line of midlateral pigment dashes develops on the tail, posteriorly between the dorsal and ventral midline pigment. The lateral row expands anteriad, reaching the trunk by the end of flexion. Pigment becomes heaviest posteriorly, and when midlateral, midventral, and middorsal melanophores are expanded in this region, an incomplete bar is formed. Concurrent with the development of the lateral midline pigment, internal series of melanophores form above and below the vertebral column and expand anteriorly in concert with the external lateral series.

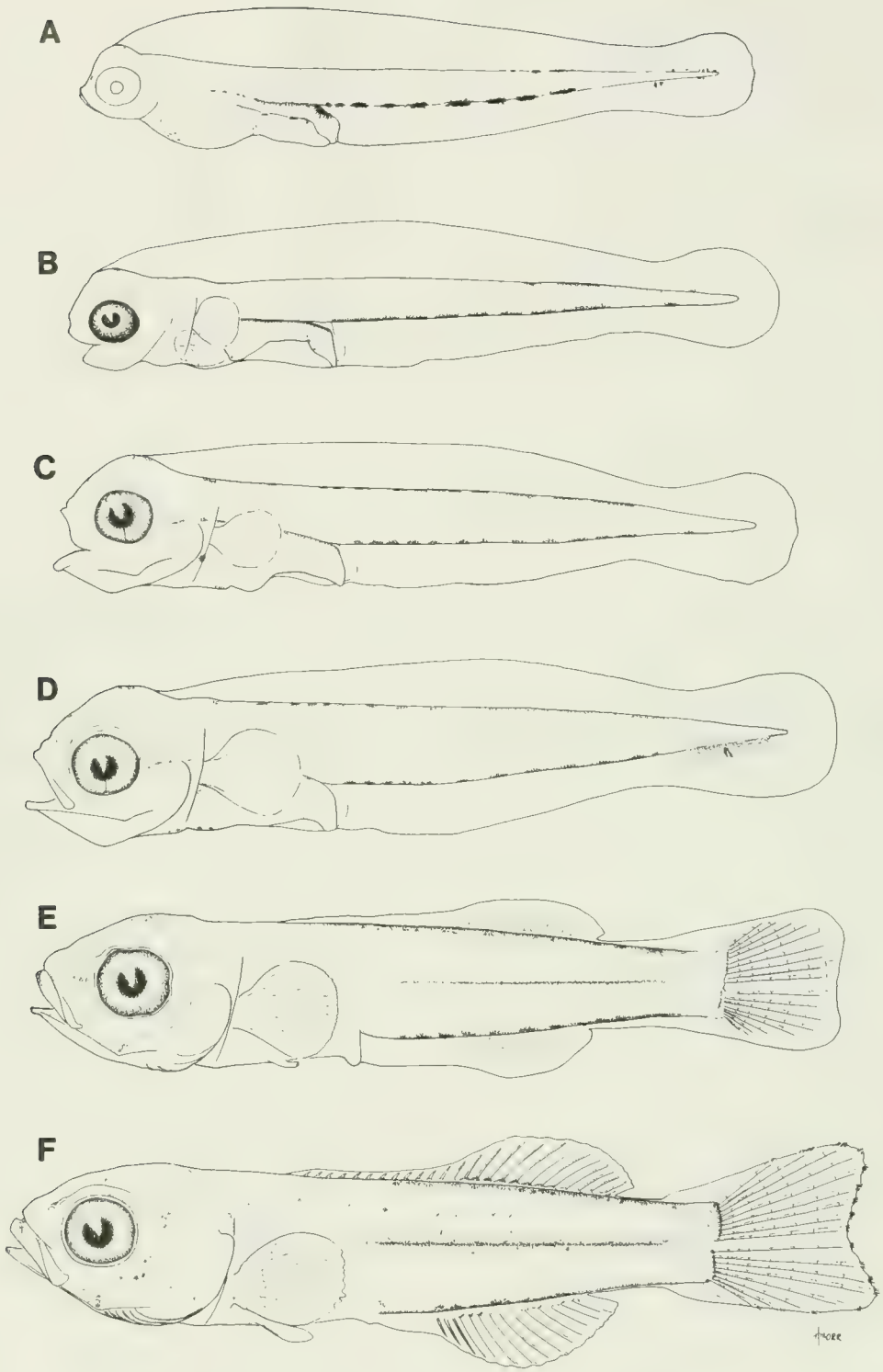

FIGURE 2.—Reared larvae of *Girella nigricans*: (A) 3.8 mm NL, day 1; (B) 3.8 mm NL, day 2; (C) 4.6 mm NL, day 8; (D) 5.3 mm NL, day 10; (E) 7.8 mm SL, day 18; (F) 10.9 mm SL, day 22.

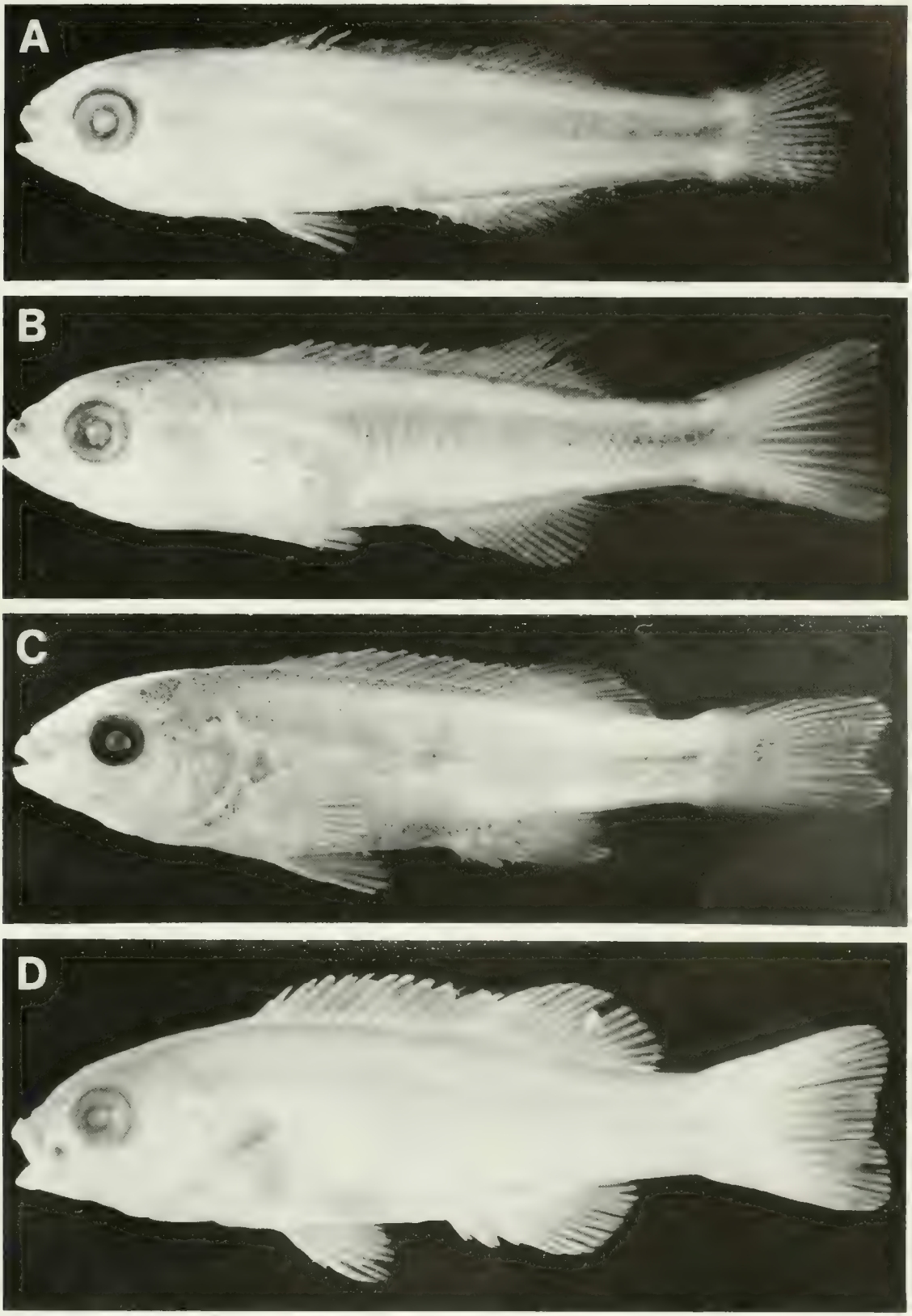

FIGURE 3.—Pelagic juveniles of *Girella nigricans*: (A) 15.8 mm SL, CalCOFI cruise 8197-JD, station 93.3.55, surface tow; (B) 17.3 mm SL, CalCOFI cruise 8107-JD, station 80.55, surface tow; (C) 22.8 mm SL, SIO Marine Vertebrate Collection, Cat. No. 76-295; (D) 29.0 mm SL, MEC SONGS cruise I-28, surface tow.

The caudal melanophore (Fig. 2D) becomes located at the posterior hypural margin between the superior and inferior elements, and remains prominent during flexion. By the end of flexion it is accompanied by 1–5 more melanophores which outline the posterior edge of the hypural plate.

By the end of flexion the sides of the gut are covered with melanophores, the dorsal midline pigment is continuous to the head, and the lateral midline series extends slightly forward of the vent. A line of pigment extends along the isthmus; pigment outlines the jaw on its ventral surface; and pigment increasingly covers the snout, dorsal surface of the head, opercles, pectoral fin bases, and the walls of the gill chambers.

During postflexion and early juvenile stages the amount of head and body pigment continues to increase. The lateral body stripe enlarges dorsad, ventrad, and anteriad. Small melanophores begin to outline the myosepta, initially in the epaxial zone and later in the hypaxial zone. Eventually the areas between the myosepta fill with melanophores and the entire body and head are covered (Fig. 3D). In addition to the development of melanistic pigment, early juveniles develop a layer of guanine which produces a silvery sheen on the lower half of the body. This silvery condition is retained throughout the pelagic phase and is lost abruptly when the pelagic young enter the tidepools at 25 mm length (Feder et al. 1974).

Fin pigment appears in early juveniles when the dorsal spines become outlined with mela-

TABLE 4.—Measurements (mm) of larvae and pelagic juveniles of *Medialuna californiensis*. Broken lines enclose specimens undergoing notochord flexion and specimens below solid line are pelagic juveniles.

Station	Body length	Snout-anus length	Head length	Head depth	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Predorsal length	Prepelvic length
5407–97.30	2.6	0.90	0.39	0.48	0.08	0.20	0.38	—	—	—	—
6607–87.55	2.8	1.2	0.60	0.58	0.08	0.22	0.44	0.30	0.14	—	—
7805–70.90	3.1	1.2	0.66	0.56	0.10	0.26	0.54	0.28	0.10	—	—
6606–90.60	3.3	1.2	0.50	0.50	0.08	0.23	0.44	0.24	0.10	—	—
6606–87.33	3.5	1.4	0.68	0.54	0.10	0.28	0.48	0.38	0.14	—	—
6907–93.30	3.8	1.6	0.84	0.74	0.22	0.32	0.68	0.44	0.18	—	—
6907–93.30	4.0	1.7	1.0	0.76	0.22	0.34	0.72	0.40	0.18	—	—
5104–107.70	4.3	1.7	0.98	0.90	0.19	0.38	0.80	0.42	0.14	—	—
6107–83.65	4.6	1.9	1.1	0.90	0.18	0.40	0.88	0.45	0.32	—	—
6207–100.45	5.0	1.9	1.2	0.96	0.24	0.44	0.84	0.60	0.20	—	—
6207–100.35	5.2	2.0	1.2	1.1	0.26	0.48	1.0	0.50	0.28	—	—
8105–100.70	5.5	2.2	1.2	1.2	0.32	0.50	1.1	0.60	0.40	—	—
5507–103.70	5.8	2.4	1.4	1.2	0.35	0.66	1.2	0.60	0.40	2.1	—
8105–100.35	6.0	2.4	1.2	1.2	0.32	0.58	1.2	0.60	0.35	—	—
6507–100.40	6.5	2.5	1.8	1.2	0.44	0.60	1.2	0.88	0.40	3.4	—
8105–100.70	6.7	2.9	1.7	1.7	0.40	0.80	1.6	0.76	0.56	3.5	—
8107–86.7.50	7.2	3.4	2.3	1.6	0.44	0.88	1.8	0.88	0.52	3.5	2.6
8108–100.40	7.9	4.0	2.4	1.8	0.64	0.88	2.0	1.3	0.48	2.9	2.8
7808–67.65	8.1	3.6	2.3	1.7	0.54	0.76	1.8	1.0	0.52	3.6	2.5
5907–103.50	8.4	4.1	2.5	2.0	0.48	0.88	2.0	1.0	0.60	3.6	3.0
7808–67.65	9.0	4.2	2.6	2.0	0.56	0.96	2.0	1.2	0.64	4.7	3.0
7808–67.65	9.2	4.1	2.4	2.0	0.42	0.96	2.0	1.3	0.64	4.1	2.9
7808–67.65	9.5	4.9	3.3	2.3	0.60	1.0	2.3	1.4	0.72	4.0	3.1
7808–93.45	9.8	5.2	3.2	2.4	0.64	1.1	2.5	1.9	0.64	4.1	3.1
5208–90.45	10.0	5.2	2.8	2.2	0.60	1.1	2.4	1.7	0.60	3.5	3.6
7808–93.45	10.8	6.0	3.5	2.7	0.72	1.2	3.0	2.4	0.62	4.2	4.1
5208–110.60	11.8	6.8	3.8	3.2	0.72	1.3	3.5	2.4	0.76	4.6	4.3
5208–110.60	12.9	7.3	4.2	3.1	0.72	1.3	3.6	2.8	0.84	5.0	5.1
7808–100.45	13.2	7.8	4.6	3.8	1.0	1.4	4.0	2.9	0.88	5.2	5.3
5208–90.45	13.5	7.8	4.7	3.8	0.96	1.5	4.0	3.3	0.96	5.3	5.2
7210–90.70	13.7	7.8	4.9	4.0	1.1	1.6	4.1	3.0	0.84	5.4	5.2
5208–90.45	17.9	9.7	5.6	4.8	1.1	1.9	5.3	4.3	0.96	6.5	6.7
7210–90.70	21.5	11.3	7.1	5.5	1.3	2.0	6.2	4.5	1.1	7.3	8.1

nophores. Gradually the fin membrane becomes covered with melanophores as does the basal half of the soft dorsal fin. Anal fin pigment is limited to a few anterior melanophores, and the caudal and the paired fins remain unpigmented.

Medialuna californiensis

Figures 1, 4, 5

General Morphology

The smallest yolk-sac larva in our collection is 2.6 mm long; it has a large oval yolk sac, a single posteriorly located oil globule (0.20 mm diameter), unpigmented eyes, and lacks a mouth (Fig. 4A). Larvae are ca. 3.0 mm long at the completion of yolk absorption; development is gradual with no abrupt changes in body form (Tables 2, 4).

The first head spines appear during flexion on the posterior preopercular margin near the angle. A 6.1 mm larva has 2 spines. The number of spines increases up to 6 in preflexion larvae and to 10–13 spines in juveniles up to 21.5 mm. In larger juveniles the spines are blunt and the posterior preopercular margin is smooth in a 33.7 mm juvenile. A single spine is present on the anterior preopercular ridge in a 6.5 mm larva. This spine is variously present or absent in flexion and postflexion larvae, and is absent in juveniles larger than 13.8 mm in our collections. A single spine is present at the edge of the subopercle in larvae as small as 7.1 mm and is found on all postflexion larvae and juveniles up to a length of 21.5 mm. An interopercular spine is present in all postflexion larvae and in juveniles up to 18.2 mm. A supracleithral spine appears late in the postflexion stage (at 10.1 mm) and a posttemporal spine appears at 12.8 mm. Both spines are present in juveniles up to 21.5 mm but are absent in larger specimens. An opercular spine is present in juveniles between 12.8 and 21.5 mm. A cleithral spine is present on a single 18.2 mm juvenile.

Notochord flexion begins at ca. 5.8 mm and is completed at ca. 8.6 mm (Table 5). Transformation into the pelagic juvenile occurs at ca. 12 mm (Fig. 5).

Fin Formation and Meristics

The first rays to form are the principal caudal rays early in flexion (Table 5). The full complement of 9+8 rays is present at midflexion, when the procurrent rays begin to develop. The full complement of 11–13 + 10–11 procurrent rays is present in early juveniles.

Dorsal, anal, and pectoral rays begin to calcify during midflexion in the manner described for *G. nigricans*. Full complements of dorsal (IX–X, 22–27) and anal (III, 17–21) rays form in early postflexion larvae (Table 5). The full complement

TABLE 5.—Meristics of cleared and stained specimens of *Medialuna californiensis*. Broken lines enclose specimens undergoing notochord flexion and specimens below solid line are pelagic juveniles.

Length (mm)	Principal caudal fin rays		Procurrent caudal fin rays		Branchiostegal rays		Pectoral fin rays		Dorsal fin rays	Anal fin rays	Pelvic fin rays		Vertebrae
	Superior	Inferior	Superior	Inferior	Left	Right	Left	Right			Left	Right	
6.1	6	5	—	—	4	4	—	—	—	—	—	—	12
6.5	9	8	—	—	6	6	—	—	—	—	—	—	21
7.1	9	8	1	1	7	7	10	10	20	II,16	—	—	24
7.4	9	8	1	1	7	6	8	8	19	14	—	—	24
8.1	9	8	—	1	6	6	6	6	9	9	—	—	24
8.6	9	8	2	2	7	7	10	10	VI,22	II,18	—	—	25
9.1	9	8	3	3	7	7	14	14	IX,22	III,18	—	—	25
9.5	9	8	4	4	7	7	14	14	VIII,22	III,17	I,2	I,2	25
10.1	9	8	5	5	7	7	14	14	X,24	III,19	I,4	I,4	25
11.0	9	8	6	6	7	7	17	17	X,23	III,18	I,5	I,5	25
12.8	9	8	9	8	7	7	18	18	X,24	III,19	I,5	I,5	25
13.8	9	8	11	10	7	7	17	17	X,25	III,19	I,5	I,5	25
18.2	9	8	13	11	7	7	18	18	X,25	III,19	I,5	I,5	25
21.5	9	8	12	11	7	7	18	18	X,25	III,19	I,5	I,5	25
27.6	9	8	12	11	7	7	18	17	X,23	III,18	I,5	I,5	25
33.7	9	8	12	11	7	7	19	20	X,23	III,18	I,5	I,5	25

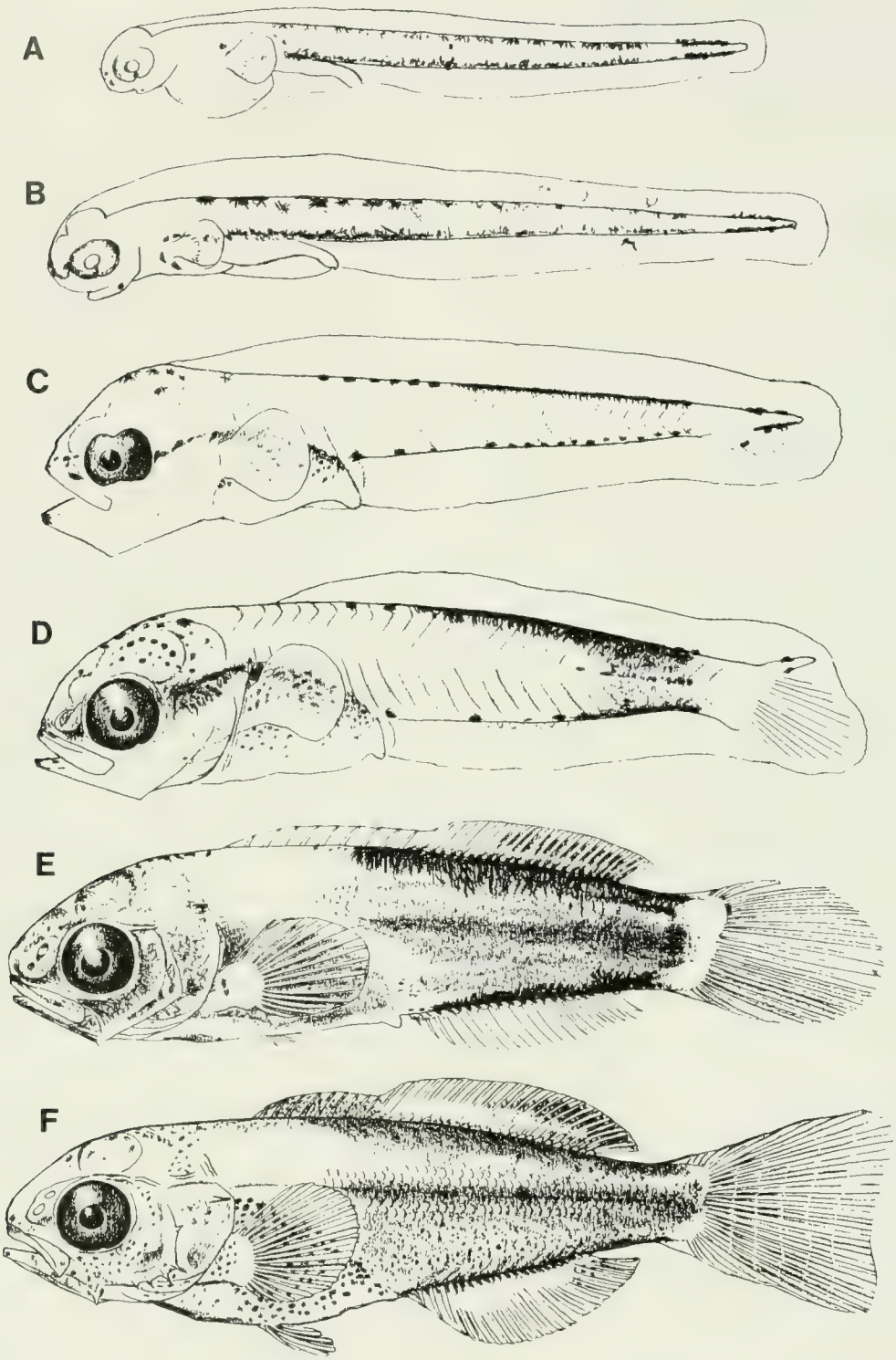

FIGURE 4.—Larvae of *Medialuna californiensis* from CalCOFI oblique plankton tows: (A) 3.0 mm NL, cruise 5004, station 120.90; (B) 3.5 mm NL, same station as above; (C) 4.7 mm NL, cruise 4906, station 102.75; (D) 6.8 mm NL, cruise 4907, station 92.68; (E) 10.1 mm SL, cruise 5007, station 100.70; (F) 11.8 mm SL, cruise 4910, station 82.77.

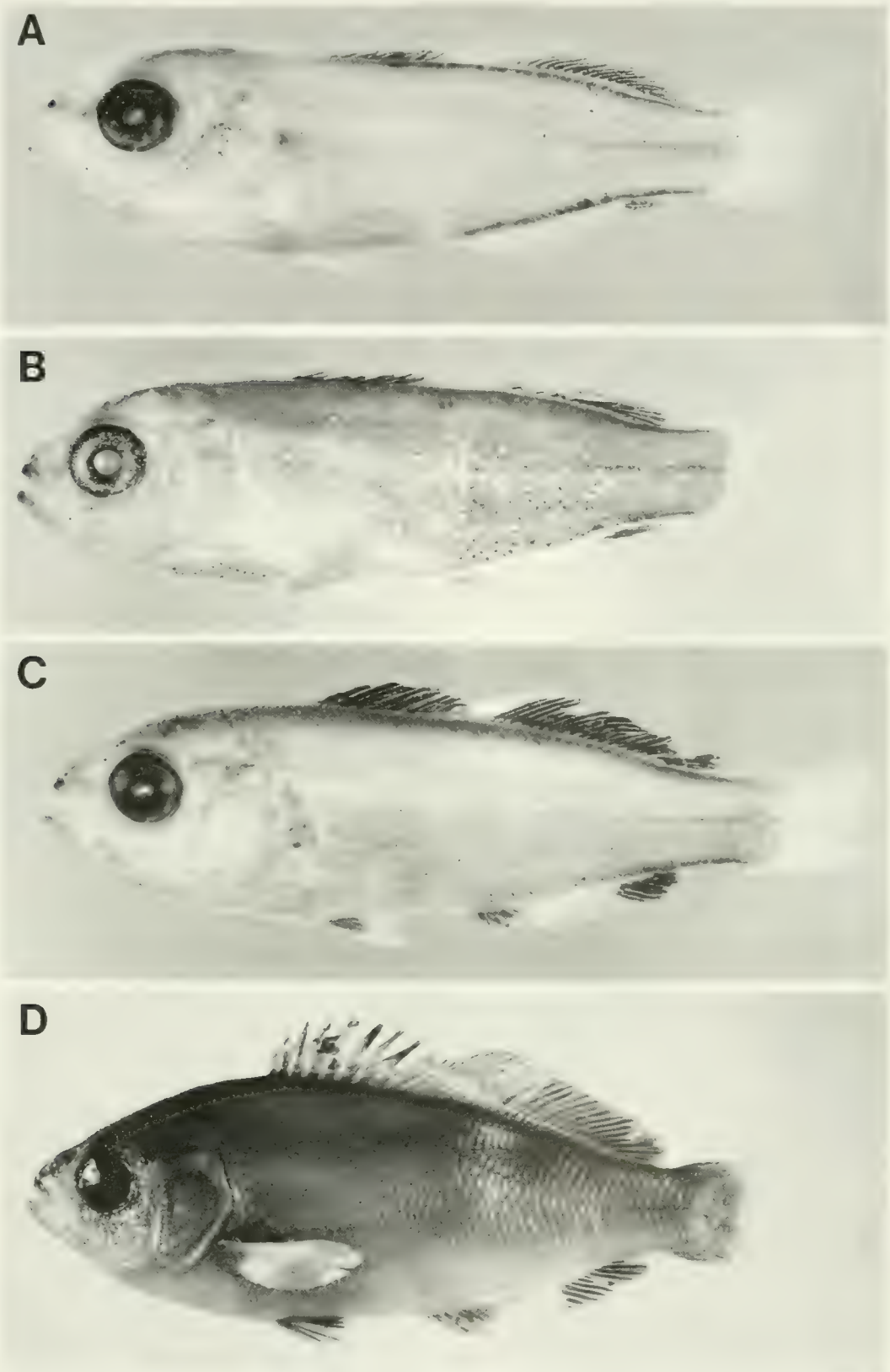

FIGURE 5.—Pelagic juveniles of *Medialuna californiensis*: (A) 13.2 mm SL, CalCOFI cruise 7808, station 100.45, surface tow; (B) 17.9 mm SL, CalCOFI cruise 5208, station 90.45, surface dipnet; (C) 20.5 mm SL, CalCOFI cruise 5407–H, station 130.60, surface dipnet; (D) 46.0 mm SL, SWFC DSJ midwater trawl, off Catalina Island, 31 October 1968.

of 17–20 pectoral rays appears at transformation. Pelvic rays begin to calcify late in postflexion and all are calcifying at transformation. Initial vertebral ossification occurs early in the flexion stage and the full complement of 25 vertebrae is present at the end of flexion. Calcification of branchiostegal rays begins late in preflexion and the full complement of 7 pairs is present in some midflexion specimens.

Pigmentation

The earliest yolk-sac larvae in our collections have extensive dorsal and ventral midline pigment. The dorsal midline has an irregular row of 30–40 melanophores between the notochord tip and the midgut region. More than 40 melanophores form an irregular series along the entire ventral margin of the tail, extending some distance forward above the gut. Melanophores in these rows coalesce to ca. 30 in each, before the eyes become pigmented. At initial eye pigmentation there are ca. 20 larger, regularly arranged melanophores in each row with a gap separating a line of 5–7 smaller melanophores that outline the dorsal and ventral margins of the notochord tip. Melanophores also appear at the dorsal surface of the gut, at the gular region, and on the snout.

At the end of the yolk-sac stage the melanophores in the dorsal and ventral rows coalesce to as few as 18 in the dorsal row and to 16 in the ventral row. A melanophore forms at the nape and, in some specimens, is continuous with the dorsal midline series. The zone of melanophores covering the dorsal surface of the gut extends forward into the head below the otic region. Embedded melanophores form in the snout region below the forebrain and some appear above the midbrain. The ventral gut melanophores move internally anterior to the gut mass. A melanophore is present at the tip of the lower jaw.

The midline melanophores coalesce further during early preflexion (15–18 dorsally and 12–15 ventrally). The short rows at the notochord tip are also reduced (2–3 dorsally and 1–3 ventrally). Melanophores are added above the brain and cover the optic lobes. Snout and otic pigment increase to give the appearance of a band through the eye, similar to that formed in *G. nigricans* and *H. azurea* (Fig. 1D, 4C). The dorsal gut melanophores increase to form a shield which extends laterally over the gut; the ventral surface of the gut remains unpigmented.

Midlateral melanophores begin to form posteriorly on the tail in preflexion larvae as small as 3.8 mm. The series consists of 1–2 (up to 4) melanophores during most of the preflexion period. During this period the dorsal midline series recedes posteriad to above the hindgut and a gap develops in the ventral series posterior to the large melanophore embedded above the anus. In late preflexion and flexion larvae the ventral series is restricted to the posterior half of the tail and contains 6–10 melanophores. Melanophores are added to the lateral series during flexion and a short bar is formed when these, together with the midline melanophores above and below, are expanded. By the end of flexion it is difficult to distinguish individual melanophores in any of the midline series. The melanistic shield on the gut covers all but the ventral midline. The dorsal surface of the head is fully pigmented and a patch of melanophores forms on the opercle. The notochord tip usually has 1–2 small melanophores dorsally and ventrally in flexion larvae, 0–2 in postflexion specimens, and 0–2 in some pelagic juveniles up to 14.5 mm in length.

The dorsal and ventral midline pigment series extend forward in postflexion larvae, the ventral series reaching the anus at ca. 9.5 mm and the dorsal series reaching the head at ca. 10.5 mm. The lateral midline series reaches the anal fin origin at ca. 9.0 mm and extends to above the midgut in transforming larvae. A covering of superficial melanophores develops on the tail and advances anteriad with the midline series. The entire body, except for the anterior trunk region, is pigmented by the end of postflexion and only a small portion of the upper trunk lacks melanophores in transforming specimens. Melanophores are added to the opercular and preopercular regions, the lower jaw, gular region, and isthmus. The entire head and gut are pigmented by the beginning of transformation.

The distinctive fin pigmentation of pelagic juveniles begins to form in late postflexion larvae when the membrane between the posterior dorsal soft rays becomes pigmented (Fig. 4E, 4F). By the end of transformation the membrane between the dorsal spines also becomes pigmented, leaving an unpigmented zone in the middle of the fin. Also, at this stage a melanistic zone develops posteriorly on the anal fin (Fig. 5A). A patch develops over the anal spines and basally on each pelvic fin in 14.0 mm pelagic juveniles; juveniles up to about 40 mm are characterized by this interrupted pattern on the median fins (Fig. 5C). In 40–50 mm juveniles the

entire dorsal fin is pigmented except for an area on the anterior half of the soft dorsal. The pelvic fins are completely pigmented at 50 mm. The pectoral and caudal fins are unpigmented in larvae and pelagic juveniles.

Hermosilla azurea

Figures 1, 6, 7

General Morphology

The size and state of development at hatching are unknown. The smallest larva examined, 2.5 mm, had pigmented eyes, a functional mouth, and no remnants of yolk or oil droplets. Preflexion larvae are moderately robust, with a coiled gut extending slightly beyond midbody (Tables 2, 6) and with a small swimbladder over the anterior gut. The head is moderately large, with a blunt snout, and with round to slightly elongate (horizontally) eyes. Development is gradual with no abrupt changes in body form or proportions. Most body parts showed small increases in size relative to the standard length (Table 2). Among the largest proportional changes are the increases in snout-anus length and in body depth (Fig. 6).

Larvae acquire only a few small head spines. The first spine may develop at the angle of the posterior preopercular margin as early as late preflexion (3.7 mm), or may be delayed until early flexion (always present by 4.7 mm); 19% of preflexion larvae had this spine. During flexion 1–3 additional small spines develop along the posterior preopercular margin and up to 3 (usually 0 or 1) small spines are acquired along the anterior preopercular ridge. Postflexion larvae may develop up to 4 very small spines along the posterior margin of the subopercular, and usually lose the anterior preopercular spines. Juveniles lack both the preopercular and the subopercular spines.

TABLE 6.—Measurements (mm) of larvae and pelagic juveniles of *Hermosilla azurea*. Broken lines enclose specimens undergoing notochord flexion and specimens below solid line are pelagic juveniles.

Station	Body length	Snout-anus length	Head length	Head depth	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Predorsal length	Prepelvic length
SONGS	2.5	1.2	0.56	0.64	0.08	0.28	0.44	0.28	0.16	—	—
	2.8	1.4	0.76	0.72	0.20	0.32	0.60	—	0.24	—	—
	3.0	1.6	0.84	0.72	0.16	0.36	0.64	0.32	0.28	—	—
	3.2	1.8	1.0	0.88	0.24	0.36	0.80	—	0.24	—	—
	3.4	1.7	0.92	0.56	0.16	0.36	0.72	0.40	0.28	—	—
	3.6	1.8	1.1	0.72	0.28	0.40	0.88	0.44	0.24	—	—
	3.8	2.1	1.2	0.96	0.32	0.44	1.0	—	0.24	—	—
	4.0	1.8	1.1	0.92	0.24	0.44	0.88	0.56	0.36	—	—
	4.4	2.1	1.1	0.92	0.28	0.44	0.92	0.52	0.36	—	—
	4.6	2.4	1.4	1.2	0.24	0.52	1.2	0.60	0.40	—	—
SONGS	4.1	2.2	1.4	1.0	0.36	0.48	1.0	0.42	0.40	—	—
	4.3	2.4	1.4	0.88	0.36	0.52	1.0	0.64	0.44	1.7	—
	4.5	2.4	1.3	1.1	0.28	0.52	1.1	0.48	0.40	1.6	—
	4.7	2.3	1.2	1.0	0.28	0.48	1.0	0.60	0.40	1.8	—
	5.0	2.6	1.6	1.2	0.40	0.60	1.3	0.48	0.48	2.0	—
	5.2	3.0	1.9	1.6	0.52	0.68	1.4	0.80	0.44	2.1	1.9
	5.4	3.2	2.0	1.4	0.48	0.68	1.5	0.80	0.48	2.3	2.0
	5.8	3.1	1.6	1.3	0.40	0.60	1.4	0.80	0.52	2.4	2.1
SONGS	6.4	3.6	1.9	1.6	0.52	0.76	1.6	1.0	0.60	2.6	2.4
SONGS	6.5	3.7	2.2	1.7	0.52	0.80	1.6	0.88	0.60	2.7	2.4
SONGS	8.6	4.9	2.5	2.2	0.68	1.0	2.2	1.7	0.68	3.3	3.4
8108–106.7.35	9.2	5.3	3.0	2.1	0.68	1.2	2.3	—	0.68	3.6	3.4
SONGS	9.6	5.5	2.9	2.6	0.68	1.1	2.5	2.0	0.64	3.7	3.9
8108–106.7.31	10.8	6.4	3.7	3.0	0.80	1.4	3.0	1.2	0.76	4.7	4.6
SONGS	14.3	8.6	4.3	3.7	1.0	1.6	4.2	4.0	0.96	5.8	5.3
SONGS	15.7	9.2	5.4	3.8	1.0	1.9	5.0	4.0	1.2	6.3	5.8
8108–120.25	17.0	9.5	5.8	4.2	1.2	2.0	5.4	4.2	1.2	7.1	6.9
SONGS	21.5	12.2	7.1	5.8	1.2	2.2	6.8	4.7	1.6	8.3	8.3

Developmental milestones occur at a relatively small size in *H. azurea*: notochord flexion begins at ca. 4.1–4.6 mm and is complete at ca. 5.9–6.3 mm; transformation to the juvenile occurs at ca. 10.8–14.3 mm (Fig. 7). Although spinous scales have been reported to occur in larvae of some Kyphosidae (Johnson 1984), juvenile *H. azurea*, as well as *G. nigricans* and *M. californiensis*, lack spines on their scales.

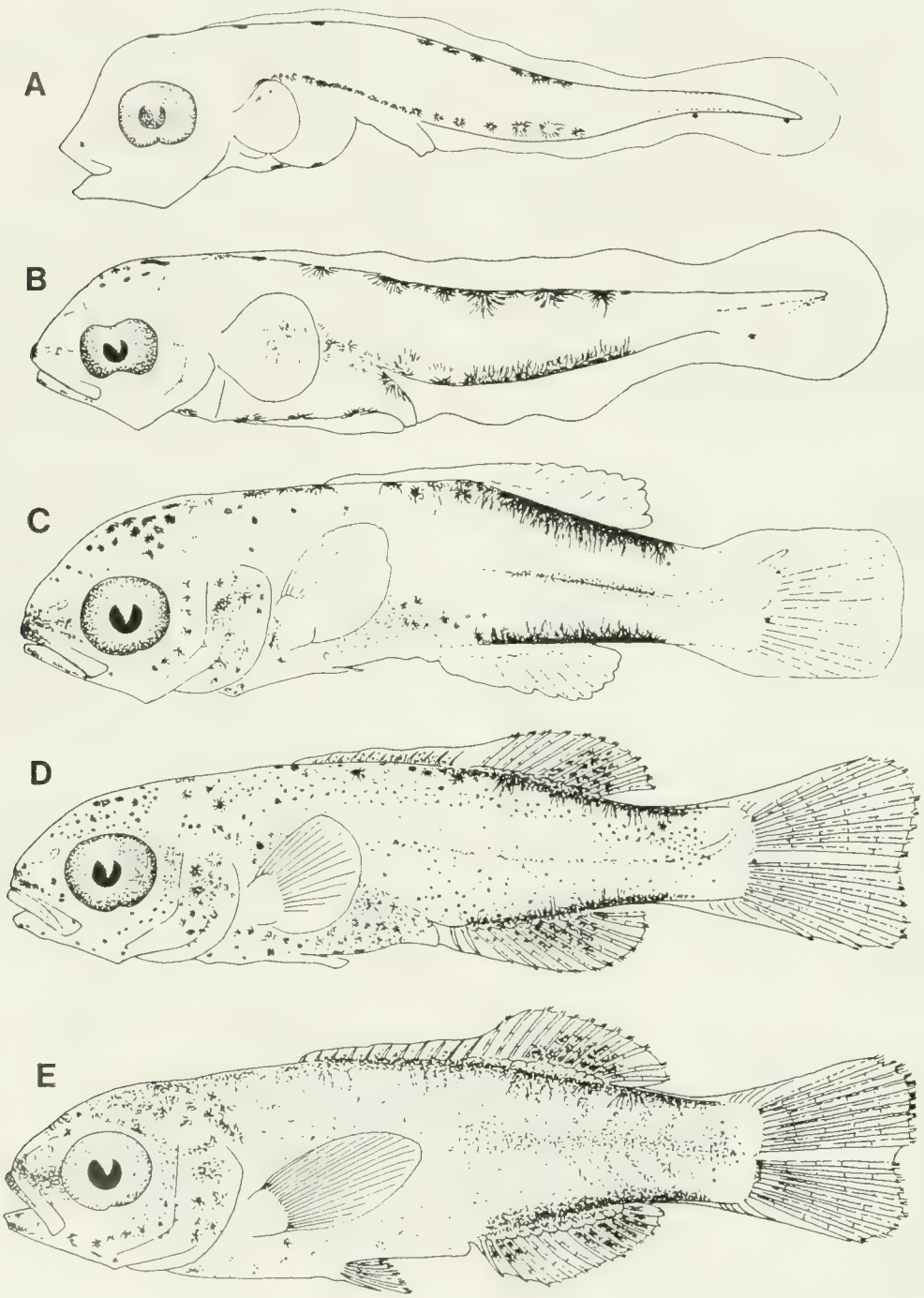

FIGURE 6.—Larvae of *Hermosilla azurea* from MEC SONGS (A–D) and CalCOFI (E) Cruises: (A) 2.6 mm NL, I–74, I-80, D–SONGS, oblique tow, 11 August 1980; (B) 4.3 mm NL, I-80, D–SONGS, surface tow, 22 September 1980; (C) 6.4 mm NL, I–53, E–LS, surface tow, 21 September 1979; (D) 8.7 mm SL, I–90, B–LS, surface tow, 27 August 1982; (E) 9.9 mm SL, 8108–NH, station 106.7.31, surface tow.

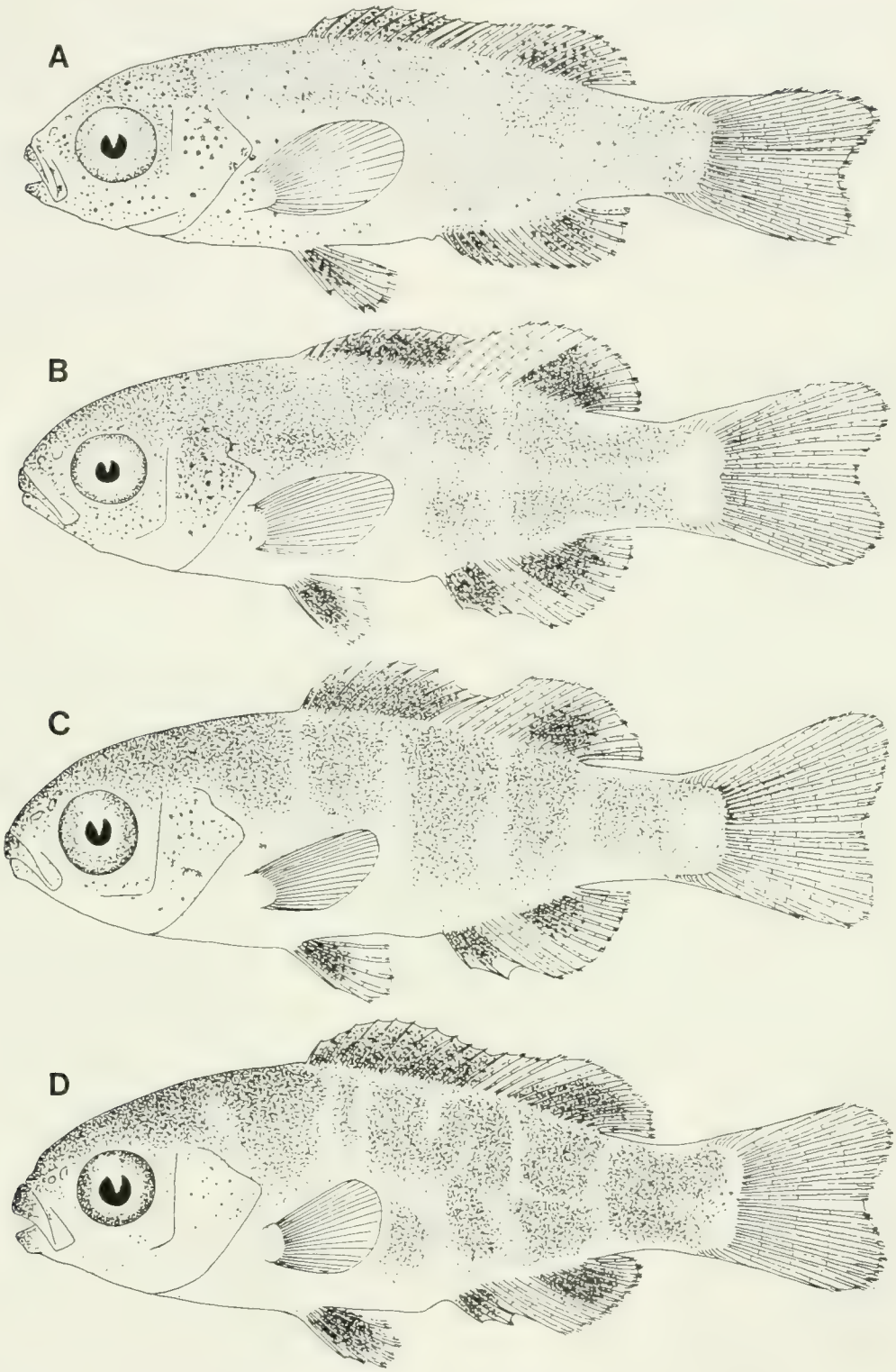

FIGURE 7.—Pelagic juveniles of *Hermosilla azurea* from MEC SONGS (A, B, D) and CalCOFI (C) surface tows: (A) 15.0 mm SL, I–35, C–1–N, 2 October 1978; (B) 16.0 mm SL, I–35, E–1–N, 2 October 1978; (C) 17.7 mm SL, 8108–NH, station 120.25; (D) 21.4 mm SL, I–35, B–1–N, 2 October 1978.

Fin Formation and Meristics

The first rays to calcify are the central principal caudal rays beginning in preflexion at about 4.1 mm (Table 7). The full complement of 9+8 principal rays is acquired during flexion at ca. 5.6 mm. Procurrent rays also may begin to calcify during flexion, as early as 5.6 mm, although more commonly they are not apparent until postflexion at ca. 6.4–6.5 mm. The full complement of 10+10 procurrent rays is completed early in the juvenile stage, by 14.3 mm.

The first dorsal and anal rays form simultaneously, early in flexion, beginning by 5.2–5.3 mm. Dorsal rays are added from anterior to posterior, with the full complement of 11 present by 5.6 mm, before the end of flexion. Dorsal spines calcify from posterior to anterior, beginning in flexion at 5.6 mm, with the full complement of 11 present in postflexion larvae by 9.4 mm. Anal rays are added from anterior to posterior, with the full complement of 10 present in flexion larvae ca. 5.3 mm long. Anal spines are added from posterior to anterior, beginning during flexion at ca. 5.6 mm; the third anal spine calcifies from the first anal ray; all three spines are present early in the juvenile stage, by 14.3 mm.

The pectoral fins initially are rounded with rounded bases, but begin to elongate during flexion when the first upper rays calcify. Addition of pectoral fin rays is from top to bottom of the fin, beginning at ca. 5.2 mm, with the full complement of 15 present by the early juvenile stage. The pelvic fins are the last to begin calcifying in the flexion stage by ca. 6.4 mm. The full complement of I, 5 rays is present by 9.4 mm.

Branchiostegal rays begin to ossify in preflexion larvae at about 4.1 mm; the full complement of 7 rays on each side is ossifying during flexion at ca. 5.2 mm. Vertebral ossification begins by 4.6 mm, just before flexion. Ossification is from anterior to posterior; all 25 centra are ossifying by the end of flexion.

Pigmentation

Preflexion larvae are relatively heavily pigmented, principally over the gut and along the dorsal and ventral midlines. In the smallest specimen examined (2.5 mm), the dorsal midline pigment consisted of a single row of 7 large stellate melanophores irregularly arranged from the midbrain to myomere 20. The number of melanophores in this dorsal row increases, so that by the beginning of flexion the dorsal and upper dorsolateral surfaces of the trunk and tail (except the last 4 or 5 myomeres) are almost completely pigmented. Dorsal and dorsolateral pigmentation on the trunk and tail becomes in-

TABLE 7.—Meristics of cleared and stained specimens of *Hermosilla azurea*. Broken lines enclose specimens undergoing notochord flexion and specimens below solid line are pelagic juveniles.

Length	Principal caudal fin rays		Procurrent caudal fin rays		Branchiostegal rays		Pectoral fin rays		Dorsal fin	Anal fin	Pelvic fin rays		Vertebrae
(mm)	Superior	Inferior	Superior	Inferior	Left	Right	Left	Right	rays	rays	Left	Right	
2.6	—	—	—	—	—	—	—	—	—	—	—	—	—
4.1	1	1	—	—	—	—	—	—	—	—	—	—	—
4.1	—	—	—	—	2	2	—	—	—	—	—	—	—
4.6	6	5	—	—	4	4	—	—	—	—	—	—	15
4.6	6	6	—	—	5	5	—	—	—	—	—	—	15
4.6	6	5	—	—	4	4	—	—	—	—	—	—	16
4.9	4	5	—	—	4	4	—	—	—	—	—	—	16
5.2	7	7	—	—	6	6	—	—	7	8	—	—	21
5.2	6	6	—	—	5	5	—	—	—	—	—	—	20
5.3	8	8	—	—	6	6	—	—	5	8	—	—	21
5.3	8	8	—	—	6	6	—	—	10	10	—	—	22
5.6	9	8	1	1	6	6	6	6	III,11	I,10	—	—	23
6.0	9	8	—	—	6	6	8	8	V,11	II,10	—	—	25
7.4	9	8	3	3	6	6	13	12	X,11	III,10	3	3	25
9.4	9	8	6	6	7	7	15	15	XI,11	III,10	I,5	I,5	25
22.2	9	8	10	10	7	7	15	15	XI,11	III,10	I,5	I,5	25

creasingly dense and spreads posteriorly; at the end of flexion the last three myomeres are usually unpigmented but acquire pigment by the end of the larval stage.

Midbrain pigment increases in concert with the dorsal trunk and tail pigment, covering the area over the midbrain and spreading anteriorly to the snout and posteriorly over the hindbrain. Thus, by the beginning of flexion, larvae are nearly completely pigmented along the upper surface (Fig. 1H). Snout and nape pigment are usually lighter than the remaining dorsal pigment.

Preflexion larvae have a single melanophore at the roof of the mouth; during flexion more melanophores may be added in this area. A melanophore first appears below the otic capsule in the preflexion stage (by 2.6 mm) and one develops under the anterior midbrain by 3.1 mm. Melanophores proliferate in these areas to give the appearance of a stripe through the head by, or during, flexion.

Pigment first appears on the dorsal surface of the hindbrain by 2.8 mm (one melanophore), and rapidly increases to essentially cover the dorsal surface of the hindbrain by early flexion (ca. 4.8 mm). This pigment subsequently extends posteriorly as a series of melanophores over the vertebral column.

One or two melanophores first appear at the tip(s) of the upper and/or lower jaw(s) between 2.8 and 3.1 mm. Melanophores spread along the upper jaw beginning late in preflexion or early in flexion, and along the lower jaw beginning midway or later through flexion. At ca. 2.8 mm a single melanophore appears on the gular membrane; by the beginning of flexion 3–4 additional melanophores form a longitudinal series evenly spaced along the membrane (Fig. 1G).

A single melanophore appears on the opercle late in preflexion or early in flexion (by 4.4 mm). Melanophores proliferate here to form a large pigment patch midway through flexion, and subsequently extend dorsally, ventrally, and anteriorly to cover the entire opercular area, usually by the end of flexion or early in postflexion.

The smallest specimens examined had a continuous double row of melanophores, which extended over the dorsal surface of the gut and swimbladder, and posteriorly as a single row nearly to the end of the hindgut. These specimens also had 1–6 melanophores evenly spread along the ventral midline of the gut from the anterior midgut to the anterior hindgut. The dorsal gut pigment increases, extending as far as halfway down the front and sides of the gut by the beginning of flexion, and completely covers the sides of the gut by the end of flexion. This pigment continues to spread ventrally, from anterior to posterior, meeting the midline series in postflexion larvae (between 8.6 and 9.6 mm). The series of melanophores along the ventral midline of the gut changes little during larval development. Modal numbers of melanophores in the series were 3–4 (range of 1–6) for preflexion larvae and 4 (range of 2–6) for flexion larvae.

Initially, ventral midline pigment on the tail consists of a single row of 7–10 large melanophores between the first and the 13th postanal myomeres. Usually 2 or 3 (1–4) small melanophores lie under the notochord tip; later these become located along the hypural margin (Fig. 6B, 6C). Occasionally, the first one or two postanal myomeres are unpigmented in preflexion larvae (14% of the preflexion specimens lacked pigment here), but thereafter the first postanal myomeres are always pigmented. The ventral melanophores enlarge and may increase in number during preflexion, so that by ca. 3.5 mm a melanistic band extends along the tail to ca. myomere 20 or 21.

A series of 1–3 small melanophores appears on the lateral midline of the tail at the 14th–20th myomeres late in preflexion or early in flexion (ca. 3.7–4.3 mm). Melanophores proliferate to form a band as do the ones along the dorsal and ventral midlines. Further enlargement of the ventral, lateral, and dorsal bands results in a nearly continuous tail bar during mid to late flexion. Subsequent proliferation of melanophores in this region and over the gut and trunk results in complete body pigmentation, except for the last 3–5 myomeres, by ca. midway through postflexion. Pigmentation is complete by transformation.

The dorsal and ventral midline pigment begins to spread onto the bases of the middle and posterior dorsal and anal soft rays during flexion at ca. 5.4 mm. By late flexion or early postflexion the membranes between dorsal rays 5 or 6 to 10 or 11 and between anal rays 5, 6 or 7 to 9 or 10 are pigmented. During postflexion, the base of the entire dorsal fin becomes heavily pigmented and near the end of the larval stage the membranes between the dorsal spines become pigmented (by ca. 9.6 mm). Pigmentation does not develop on the membranes between dorsal soft rays 1–5 during the larval period, and is very sparse there in juveniles. The base

of the entire anal fin is pigmented by 8.6 mm; the anal spines and membranes are heavily pigmented by 9.6 mm, as are the membranes between anal soft rays 5 to 9 or 10. The membranes between anal soft rays 1–5 are usually unpigmented in larvae, and only sparsely pigmented in juveniles.

Caudal fin pigment is usually restricted to the melanophore(s) at the distal hypural margin during the larval stage. Small melanophores may be acquired along the proximal edges of some of the principal caudal rays in small juveniles.

The first pigment on the paired fins consists of a single melanophore on the lower proximal external surface of the pectoral fin base. This melanophore may appear as early as 4.8 mm, but is not consistently present before ca. 8.6 mm. Pectoral pigment subsequently changes little, except that beginning at ca. 9.6 mm, melanophores appear at the bases of the upper pectoral rays. The pelvic fins are unpigmented in larvae but become heavily pigmented in small juveniles.

Transforming specimens are uniformly pigmented except for the residual melanistic bands at the dorsal and ventral margins and along the lateral midline of the tail. Between 11 and 14 mm, a series of faint bars begins to appear, one anterior to the dorsal fin, one below the spinous dorsal, one below the transition from spinous to soft dorsal, one below the soft dorsal, and one at the caudal peduncle (Fig. 7C). The bars are usually interrupted along the lateral midline and variously developed below the midline, giving a mottled appearance. The mottled appearance is intensified when the bars begin to subdivide and ultimately produce the 12 bars found in late juveniles and adults.

DISTRIBUTION

Girella nigricans

A total of 71 occurrences of *G. nigricans* larvae were recorded from CalCOFI oblique plankton tows during the period 1951–81 (Fig. 8). Larvae were not found on survey cruises during 1951, 1953, 1955, and 1972. Identification of some shorefish species was of variable competency during the early years of CalCOFI and this may explain the apparent absence of *G. nigricans* larvae in 1951, 1953, and 1955. Larvae ranged from San Luis Obispo, CA (cruise 6907, station 77.48) to San Cristobal Bay, Baja California (cruise 5810, station 137.23)—the former station is the only record north of Pt. Conception, CA. Thirty-eight percent of the total occurrences were between Pt. Conception and the Mexican border and 62% were off Baja California. Larvae ranged seaward to ca. 330 km (cruise 6407, station 93.70); however, 80% of the occurrences were from station 40 shoreward on the CalCOFI survey lines (typically <110 km from the coast). Numbers of larvae sorted from each sample were low, ranging from 1 to 5, with a mean of 1.35 per positive tow. The standardized mean number per positive tow was 4.0 with a range of 0.3–17.5[1]. *Girella nigricans* is a highly seasonal spawner with 80% of the larvae occurring in summer months (June, 27%; July, 45%; August, 8%). Larvae were not taken in January–March.

The importance of the surface layer as a habitat for *G. nigricans* larvae has not been assessed; however, the addition of surface (Manta net) tows on CalCOFI stations during the 1978 and 1981 surveys has provided some information. Larvae occurred in nine surface tows in 1978 and in 11 tows during 1981. These occurrences compare with those from three positive oblique tows in 1978 and one in 1981 and suggest that 1) *G. nigricans* larvae may occur frequently in the neuston and 2) they are undersampled by oblique tows. The mean size of larvae taken in surface nets is nearly twice that of larvae taken in oblique tows. The mean larval length from surface tows during 1978–81 was 7.1 mm ± 3.7 SD (range = 2.6–16.5 mm). The mean for oblique tows during 1978–81 was 3.8 mm ± 1.69 SD (range = 2.2–15.0 mm).

Medialuna californiensis

A total of 150 occurrences of *M. californiensis* larvae were recorded on CalCOFI oblique plankton tows during 1951–81 (Fig. 8). Larvae occurred on all surveys except during 1953; the apparent absence during 1953 probably was a result of identification error. Larvae ranged from off Monterey Bay, CA (cruise 5707, station 67.55) to off Pt. San Jaunico, Baja California (cruise 6507, station 133.50). There were only five occurrences north of Pt. Conception, CA, during the 30 yr period; only one of these was near the coast (Fig. 8). Except for two stations,

[1]Standardized number adjusts for percent of sample sorted and standard haul factor to give the number of larvae under 10^2 m of sea surface (see CalCOFI ichthyoplankton data reports cited in Ambrose et al. 1988).

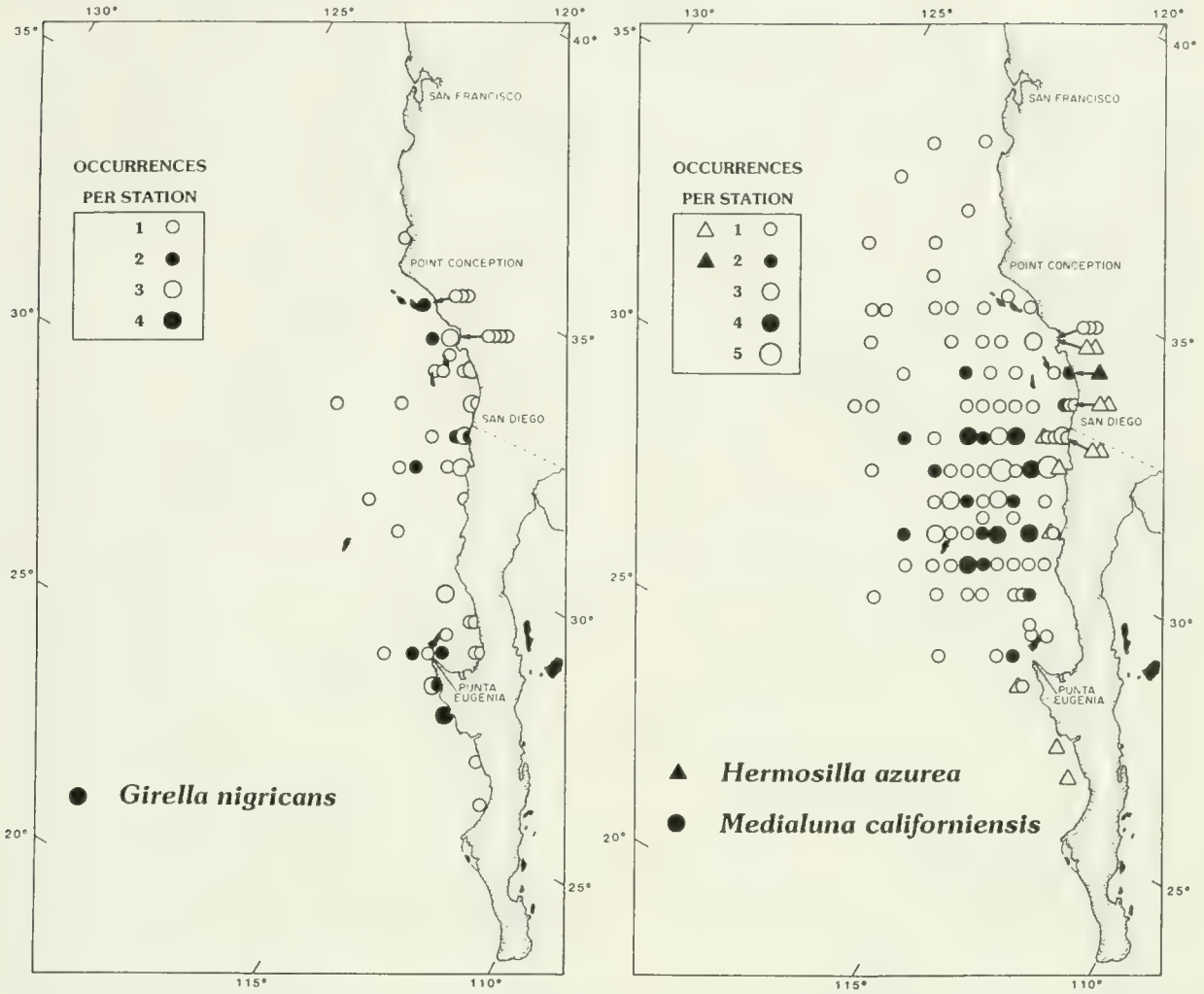

FIGURE 8.—Pooled numbers of occurrences of *Girella nigricans*, *Medialuna californiensis*, and *Hermosilla azurea* larvae taken in CalCOFI tows from 1951 to 1981. Occurrences for *G. nigricans* and *M. californiensis* represent oblique tows and those for *H. azurea* are both oblique and surface tows.

all the remaining larvae were taken between Pt. Conception, CA and Pt. Eugenia, Baja California; 28% of these occurrences were off California and the remainder were off Baja California.

In contrast to *G. nigricans* larvae, those of *M. californiensis* occur well offshore to a distance of ca. 500 km (cruise 5505, station 93.95); 71% of the occurrences were seaward of Station 40 (>110 km from the coast on most lines). Numbers of larvae ranged from 1 to 11 with a mean of 1.42 per positive tow, slightly higher than for *G. nigricans*. The standardized mean number per positive tow was 4.94 with a range of 1.0–30.7. Like *G. nigricans*, the occurrence of *M. californiensis* larvae was highly seasonal with 53% taken in July and 90% in June–August. Larvae did not occur in November–March.

Larvae of *M. californiensis*, like those of *G. nigricans*, utilize the neuston habitat and may be undersampled by oblique tows. *Medialuna californiensis* occurred only once in the oblique tows during 1978 and once in 1981, whereas there were five positive Manta tows in 1978 and three in 1981. The mean size of larvae taken in surface tows during 1978–81 was almost twice that in the oblique tows (7.0 mm ± 2.60, range = 2.6–11.0 mm versus 3.9 mm ± 1.18, range = 2.3–9.4 mm).

Hermosilla azurea

Larvae of *H. azurea* have a nearshore shallow distribution (Fig. 8). We can document only two occurrences of this species in the entire CalCOFI time series of oblique tows (cruise 6907, station 93.30, two specimens; station 97.29, four speci-

mens). Since this species was first identified during the course of the present study, it is possible that other misidentified specimens reside in the collections. They were not, however, confused with *G. nigricans* or *M. californiensis* since we have reexamined all identifications of these species. Larvae of *H. azurea* occurred in Manta net samples at three stations during the 1978 survey and at nine stations on the 1981 survey. Occurrences ranged from Santa Monica Bay, CA (cruise 8107, station 86.7.33) to Pt. San Juanico, Baja California (cruise 7807, station 133.23). Occurrences were shoreward of station 36 on each CalCOFI line (4–42 km from the coast).

Larvae of *H. azurea* were well represented in the SONGS plankton collections of MEC Analytical Systems. The shallow distribution of *H. azurea* larvae was clearly demonstrated in the SONGS collections. Surface tows accounted for 87% of the larvae and oblique tows for 14%. Larvae occurred principally in the outer section of the SONGS transect (1.9–7.2 km from the coast; ca. 18–75 m depth). Larval occurrence was highly seasonal, with 62% of the total number taken in August and >99% in July–September.

SYSTEMATICS

Johnson (1984) discussed kyphosid fishes in his review of percoid systematics and ontogeny. He considered Girellidae, Kyphosidae, and Scorpididae to be distinct families and redefined the latter to include only four genera (*Scorpis*, *Medialuna*, *Labracoglossa*, and *Bathystethus*). Evidence from adult anatomy that led to these decisions was deferred to a forthcoming review (Johnson and Fritzsche, in press). Johnson (1984) pointed out the similarity of girelline and scorpidine larvae and presented this as evidence for considering them sister groups; he now believes girellines, scorpidines, and kyphosines form a monophyletic group (G. D. Johnson[2]).

A principal problem in assessing ontogenetic characters of teleost fishes is a lack of information for all but a few taxa under consideration. This is especially true for percoids and for this group of percoids. In addition to our description of *Girella nigricans*, ontogenetic series are known for two other species of *Girella* (*G. punctata* eggs, larvae, and juveniles [Mito 1958a]; *G. melanichthys* larvae [Okiyama 1988]). Developmental stages of the other girelline genus (*Graus*) are unknown. Other than our description of *Medialuna californiensis*, the only scorpidine larval series description is that of *Labracoglossa argentiventris* (Hattori 1964). Developmental stages of two of the four kyphosine genera are known. In addition to our description of larvae and pelagic juveniles of *Hermosilla azurea* there are descriptions of developmental stages of at least three species of *Kyphosus* (*K. cinerascens* larvae and juveniles, [Mito 1958b; Okiyama 1988]); *K. sectatrix* transforming larvae and juveniles [Moore 1962]; *K. incisor* transforming larvae and juveniles [Moore 1962]; *K. vaigensis* or *bigibbus* eggs [Watson and Leis 1974]; *K. vaigensis* or *bigibbus* larvae [Miller et al. 1979; Leis and Rennis 1983]). Developmental stages of *Sectator* have not been described.

The literature on development stages of these fishes does not provide sufficient descriptive detail to adequately assess ontogenetic characters. In this paper we present detailed descriptions of representatives of the three putative families to establish a basis for character comparisons. The striking feature of the three larval series is their similarity. The fact that the three species were confused with one another during the history of CalCOFI surveys attests to this in a practical sense. Our more rigorous study of their morphologies and pigment patterns has allowed us to identify each specimen correctly, while reinforcing the similarities perceived by early CalCOFI workers. These similarities are 1) a general percoid body form with a *Girella-Medialuna-Hermosilla* grade in degree of robustness; 2) dorsal and ventral midline melanophore series, with unique variations for each species; 3) lateral midline melanophore series, with unique variation; 4) an embedded melanistic band through the eye region; 5) minute melanophores at the tip of the notochord which become associated with the hypural margin of the caudal fin; 6) an anteriad progression of general body pigmentation late in the larval period; and 7) head spination with a *Girella-Hermosilla-Medialuna* grade in degree of development. This morph is not unique among percoids (see Leis and Rennis 1983; Johnson 1984); however, the coherence of these and other more subtle characters among these three eastern Pacific species supports the argument that they represent sister groups.

The pattern of lateral pigmentation is more variable in kyphosine larvae than in girellines and scorpidines. We can recognize three pat-

[2]G. D. Johnson, Fishery Scientist, National Museum of Natural History, Washington D. C. 20560, pers. commun. April 1989.

terns of lateral body pigment in kyphosines. The pattern in *H. azurea* larvae is essentially like that in *Girella* and *Medialuna*. It begins as a midlateral series on the tail and fills in the unpigmented region above, below, and anteriad to it. In *Kyphosus sectatrix* and *K. incisor* lateral pigment extends along the entire epaxial region of the body (Moore 1962). In *K. cinerascens* and *K. vaigensis* (*bigibbus*?) larvae a broad zone of lateral body pigment expands to cover unpigmented regions above, below, anteriad, and posteriad to it (Mito 1958b; Leis and Rennis 1983).

Ontogenetic divergence among kyphosid fishes is greater during the pelagic juvenile stage than in larvae. The silvery pelagic juveniles of *Girella*, which transform abruptly to olive benthic juveniles, are well known. Apparently, *Medialuna* not only has a silvery pelagic juvenile too, but also has a strongly variegated pattern on the dorsal and anal fins. The pelagic juveniles of *H. azurea* are strongly mottled. This feature is shared with other kyphosines, some of which exhibit a striking pattern of pale spots (*K. sectatrix* and *K. incisor* [Moore 1962]; *K. cinerascens* [Mito 1958b]; *K. vaigensis* (*bigibbus*?) [W. Watson, pers. obs.]).

Ontogenetic stages of kyphosid fishes provide a promising array of systematic characters. The utility of these characters in assessing phylogenetic relationships is limited by our present inability to identify shared derived character states through outgroup comparison. The solution to this problem awaits a broader knowledge of ontogeny in kyphophids and other groups in the percoid series.

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Spatial Aspects of Imprinting and Homing in Coho Salmon, *Oncorhynchus kisutch*

T. P. Quinn, E. L. Brannon, and A. H. Dittman

ABSTRACT: Analysis of seven years of coded wire tag data revealed that juvenile coho salmon, *Oncorhynchus kisutch*, released from two hatcheries in the Lake Washington watershed return almost exclusively to their hatcheries of origin. To determine if they learn the characteristics of more than one water source prior to seaward migration, coho salmon were reared in one of three hatcheries and were released from it or, after transportation, from a release site farther downriver. The locations to which adult salmon returned indicated that they had learned both the characteristics of their release site and the hatchery where they had been held prior to release. Salmon transported around much of their migratory route returned primarily to their release site, indicating that they needed to learn sequences of odors during their seaward migration in order to home in a complex river system.

The majority of salmonid fishes that survive to adulthood return to their natal site to spawn (Foerster 1936; Shapovalov and Taft 1954; Armstrong 1974; Swain 1982; Quinn and Fresh 1984; Berg and Berg 1987; Quinn and Tallman 1987; Quinn et al. 1987). The prevalence of homing in species with highly variable patterns of freshwater residence and anadromy (Rounsefell 1958) suggests that the process by which the fish learn the characteristics of their natal environment is flexible.

Coho salmon, *Oncorhynchus kisutch*, exposed to an artificial odorant prior to downstream migration as smolts are attracted to that odor at maturity (Scholz et al. 1976; Hasler and Scholz 1983). These and other results led Hasler and Scholz (1983) to hypothesize that salmon imprint only once, immediately prior to downstream migration. However, there is also evidence that wild coho salmon move considerable distances within watersheds before migrating to sea (Peterson 1982). Adult coho return to the site where they emerged from gravel nests as fry, not the site where they resided as smolts (Lister et al. 1981). Sockeye salmon, *O. nerka*, also typically home to tributaries of lakes experienced only as embryos or fry, not to the lake and its outlet experienced as smolts (see references in Quinn et al. 1987).

Transportation of juvenile salmon and trout within river systems has had mixed effects on homing. In some cases, fish captured during seaward migration, trucked to the lower Columbia River, and released, generally returned to the upriver rearing site (Ebel et al. 1973; Slatick et al. 1975). On the other hand, displacement from a hatchery to a release site downriver has often resulted in returns to the release site (Jensen and Duncan 1971; Vreeland et al. 1975; Cramer 1981; Vreeland and Wahle 1983).

It is thus unclear whether salmon learn the chemical characteristics of a single site at a specific developmental stage ("imprinting" by smolts: Hasler and Scholz (1983)) or if they learn a sequence of olfactory landmarks (Harden Jones 1968; Brannon 1982). By displacing smolts seaward, we can create gaps in their migratory experience as a way to examine the spatial aspects of olfactory learning. Specifically, we conducted two experiments in which salmon were released at their rearing sites or at a site downriver. The locations to which these salmon returned were compared among experimental groups and also compared to data from previous years on homing and straying within the watershed.

MATERIALS AND METHODS

Data Analysis on Homing in the Lake Washington Watershed

There are two major hatchery sources of coho salmon in the Lake Washington watershed (Fig. 1): the University of Washington's (UW) hatchery and the Washington State Department of Fisheries' hatchery on Issaquah Creek (Iss). We inspected the Washington Department of Fisheries and University of Washington data bases on coded wire tagged coho salmon and identified salmon recovered at these two hatcheries for return years 1979–85 to determine the extent of straying within this system.

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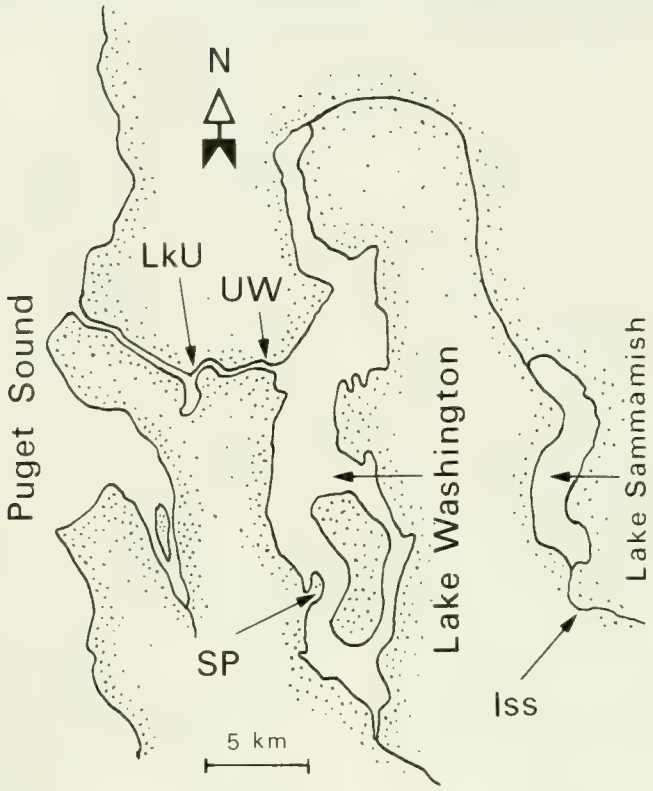

FIGURE 1.—Map of the Lake Washington watershed showing the locations of the release site on Lake Union (LkU) and the hatcheries at the University of Washington (UW), Seward Park (SP), and Issaquah Creek (Iss).

Treatment of Juveniles

In 1985 we initiated a study of patterns of imprinting and homing in the Lake Washington watershed. The basic experimental design was to expose coho salmon to the odors of Seward Park (SP) or Issaquah Creek (Iss) hatcheries and release them from those hatcheries or from a site 2.2 km downstream from the UW hatchery (Fig. 1). (The SP hatchery had been used for production of rainbow trout but not coho salmon prior to this experiment. Water for the SP hatchery is pumped from Lake Washington). Another group was reared in UW water and released at the downriver site.

Between 18 and 25 November 1985, adult coho salmon that had returned to the UW hatchery were spawned and the fertilized eggs incubated at the UW hatchery in dechlorinated city water. This is not the water source normally used in the hatchery; fish are normally incubated and reared in water pumped from the ship canal draining Lake Washington into Puget Sound (Fig. 1). The eggs hatched in January and yolk absorption was completed in March. In late March the fry were separated into three groups. Group 1, the control, was held at the UW hatchery and exposed to ship canal (UW) water during the smolt phase, from 20 May until 10–11 June, when the fish were tagged with internal coded wire tags. Fish in this study were judged to be smolts by their downstream migratory behavior and silvering. Only fish with silvery coloration and lacking parr marks were given coded wire tags. Group 1 fish were released into Lake Union, 2.2 km downstream from the UW hatchery, on 17 June. Groups 2 and 3 were transported to the SP hatchery on 21 March and reared there. They were tagged on 13 June (Group 2) and 14 June (Group 3). Group 2 fish were released into Lake Union on 1 July and Group 3 fish were released from SP on 27 June. Table 1 summarizes information on the treatments of the these groups.

On 19 March 1986 coho salmon at the Iss hatchery were marked by excision of the left or right ventral fin (10,000 fish per treatment). These salmon had emerged as fry in 1985 and smolted after one year in freshwater (average

TABLE 1.—Summary of coho salmon experimental treatments, indicating the date (in 1986) when fish were exposed to different water sources or moved. UW refers to UW hatchery water, CW refers to dechlorinated city water at the UW hatchery, SP refers to lake water at the Seward Park hatchery, Iss refers to the Issaquah Creek hatchery, and LkU refers to the Lake Union release site.

Developmental stage or operation		Experimental group				
		1	2	3	4	5
Eggs, alevins, and fry:	Site	CW	CW	CW	Iss	Iss
Parr:	Site	CW	SP	SP	Iss	Iss
	Date	—	3 21	3 21	—	—
Smolts:	Site	UW	SP	SP	Iss	Iss
	Date	5 20	—	—	—	—
Tagging:	Site	UW	SP	SP	Iss	Iss
	Date	6 10–11	6 13	6/14	3/19	3/19
Release:	Site	LkU	LkU	SP	LkU	Iss
	Date	6/17	7/1	6/27	3/19	4 9
	Size	10.0 g	12.6 g	11.3 g	26 g	26 g
	Number	8,491	10,020	10,148	10,000	10,000

weight = 26 g), unlike the UW coho, which smolted in their first spring. Those with their right fin clipped (Group 4) were trucked in two groups of 5,000 fish each to the Lake Union site and were released on 19 March. Those with the left ventral fin clipped (Group 5) were returned to the hatchery pond and released from the hatchery with the normal production fish on 9 April.

Recovery of Returning Adults

It was anticipated that most experimental coho escaping the fisheries would return to the hatcheries at UW, SP, or Iss, primarily in 1987. Coho salmon of the UW population almost all return in the second fall after their release (Brannon et al. 1982) and few precocious males ("jacks") occur. A trap to recover salmon returning to the SP hatchery was built in summer 1987; therefore no jack (1986) returns would have been collected that year, but the UW and Iss hatcheries were operating in 1986 to collect jacks. All hatcheries were also open in 1988 for salmon returning in the third fall after release. In addition to these primary recovery sites, the National Marine Fisheries Service (NMFS) operates a small hatchery on the opposite side of the ship canal. While no salmon released from NMFS were expected to return in 1987, the hatchery trap was operating and salmon entering it were checked. Some salmon released in Lake Union (where there is no hatchery or spawning ground) might have been expected to enter the NMFS facility if they had not imprinted on the UW hatchery.

RESULTS

Analysis of the historical data revealed that from 1979 to 1985, 5,465 coho salmon with coded wire tags from UW and Iss were recovered at these two hatcheries. Of 4,696 tagged UW coho salmon recovered, only two (0.04%) strayed to Iss. Similarly, of 769 tagged Iss coho, only one (0.13%) entered the UW hatchery. Thus, virtually no straying takes place between these two hatcheries when coho are reared and released at the hatcheries.

Only one jack from the UW-SP transfer groups (from Group 2) was recovered in 1986 at the UW hatchery, indicating that the absence of a return trap at SP did not bias the data significantly (Table 2). Group 1, exposed to UW water and released into Lake Union, returned exclusively to the UW hatchery (34/34). Group 2, which had not directly experienced UW water but had been reared at SP and released into Lake Union returned primarily to the UW hatchery (Table 2) but seven salmon were recovered at SP. Group 3 fish, reared in the same manner as Group 2 fish but released from SP, returned exclusively to SP.

In 1986 and 1987, 73 fish with clipped ventral fins were recovered at the UW and Iss hatcheries. Group 5, reared and released from Iss

TABLE 2.—Patterns of homing displayed by adult coho salmon from different experimental rearing regimes. Numbers listed represent actual fish returning while numbers in parentheses are the percentage of each experimental group returning to that recovery hatchery. Groups 3 and 5 were reared and released at Seward Park and Issaquah Creek hatcheries, respectively. Groups 1, 2, and 4 were released into Lake Union but had been reared at the University of Washington, Seward Park, and Issaquah Creek hatcheries, respectively.

Recovery hatchery	Experimental group				
	1	2	3	4	5
U. of Washington	34(100)	44(86)	0	15(88)	2(4)
Seward Park	0	7(14)	44(100)	0	0
Issaquah Creek	0	0	0	2(12)	54(96)

hatchery, generally returned to Issaquah Creek (54/56 recoveries). The return of transported fish (Group 4) was lower but they tended to enter the UW hatchery (15/17 recoveries). Fifteen coho salmon entered the NMFS facility in 1987 but none were from any of the experimental treatments.

DISCUSSION

The coded wire tagging data demonstrated that salmon home almost without fail to the UW and Iss hatcheries if they have been reared and released at these sites. The return of all members of Group 1 to the UW hatchery supported the findings of many previous studies (reviewed by Hasler and Scholz (1983)) that exposure to a water source at the smolt stage or at the time of release provides a sufficient basis for homing. Similarly, Group 3, released from SP, returned exclusively to SP. Fish from Group 2 had experienced a gap in their migration, relative to Group 3. They were reared at SP during the parr and smolt stages but did not experience the route from SP to the Lake Union release site, a distance of some 18 km. Most of these fish entered the UW hatchery but 7 of 51 returned to SP.

The Iss controls (Group 5) returned to that hatchery and the salmon trucked to Lake Union tended to enter the UW hatchery, though the return rate of the experimentals was quite low. The salmon held in Iss hatchery before being trucked to Lake Union presumably learned the characteristics of their hatchery but were unable to detect them when they returned to Lake Union as adults. Taken together, the results of the experiments support Harden Jones' (1968) hypothesis that salmon learn and subsequently retrace a sequence of odors. In situations where the home odor travels relatively undiluted or unchanged downriver, salmon artificially displaced downriver might be able to home successfully. However, if the home water is diluted or altered by passage through lakes (as may have occurred in our experiments), salmon may only return as far as their release site.

It is possible that the differences between the patterns of homing displayed by Groups 2 and 3 and Groups 4 and 5 could be due to differences in the degree of smolting. For example, if there is a very tight window for imprinting which is linked to some subtle (or unknown) changes during smoltification, then perhaps 7 of the 51 returning fish from Group 2 had reached and ended the imprinting phase prior to transport to Lake Union. This would imply that all the returning fish were able to detect SP water but that only the above 7 responded to it. This explanation seems unlikely, however, since these fish were released during a relatively late phase of the smolting process. If imprinting is linked to events such as natural thyroid hormone peaks and the onset of silvering and downstream migration (Hasler and Scholz 1983), then all the fish in Group 2, whether released at SP or transported to Lake Union, would have been expected to return to SP.

The gap in experience that we provided was relatively short in distance but great in effect on homing, compared with experiments on the Columbia River (e.g., Slatick et al. 1975) in which much longer displacements did not affect homing. However, extreme treatments, such as displacement 574 km downriver from Dworshak Hatchery to Bonneville Dam (Slatick et al. 1982), did impair homing. Presumably, if salmon can detect the upriver odor when they arrive at the release site, little effect of displacement will be recorded, regardless of the linear distance.

The fish displaced downriver to Lake Union as smolts tended to enter the UW hatchery even though they had not experienced its water. We hypothesize that these fish initially returned to the release site in Lake Union and found it unsuitable for spawning. The salmon could then have been attracted to the odors of the 1,708 adult coho salmon which were in the UW hatchery over the course of the season. By comparison, the equally proximate NMFS facility contained only 15 adult coho. Adult coho salmon can recognize waters conditioned by conspecifics (Dizon et al. 1973) and behavioral attraction to such species-specific odors has been documented

(Quinn et al. 1983). The return of Group 2 to Seward Park can be explained only by the fact that the salmon had been reared there. Iss hatchery produced about 12 times as many coho salmon as the UW hatchery in 1987, but no fish from Group 2 entered Iss, indicating that little wandering took place.

The patterns of freshwater residence and seaward migration vary greatly among and within salmonid species, yet homing to the natal site prevails throughout the family. There seems to be a flexible system by which site-specific odors are learned prior to and during seaward migration. Hasler and Scholz (1983) demonstrated a link between the thyroid hormones associated with smolt transformation (Dickhoff et al. 1978; Dickhoff and Sullivan 1987) and olfactory imprinting. However, the ability of salmon to learn odors on more than one occasion is not fully compatible with a single peak of thyroid hormones in spring. The solution to this problem may lie in the discovery by Dickhoff et al. (1982) that exposure of coho salmon to novel water sources at the time of year when they would migrate to sea induces transient peaks in thyroid hormone levels. Thus, if thyroid hormones are linked to olfactory learning, there may be feedback from migration to hormones, resulting in additional learning during migration. Exposure to novel waters (e.g., at the confluence of rivers) might induce elevated hormone levels and trigger learning of the water source as an olfactory way-point to be used during upstream migration years later.

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Spatial Distribution of Juvenile Salmonids in the Hanford Reach, Columbia River

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ABSTRACT: The cross-sectional distribution of juvenile chinook salmon, sockeye salmon, and steelhead was determined in the Hanford Reach of the Columbia River from July to September 1983 and from April to July 1984. Fish were sampled with fyke nets from anchored barges, movable shoreline fyke nets, seines, and with electroshocking equipment. Fall chinook salmon from naturally spawning populations and from hatchery releases were the principal species collected in the spring. Zero-age fall chinook salmon occurred primarily in shoreline areas of reduced current velocity but were present throughout the river cross section during their early rearing and outmigration period. Hatchery-released fall chinook smolts were less abundant in nearshore areas than were wild fish. Yearling spring chinook salmon, sockeye salmon, and steelhead smolts from upriver areas were collected mainly from the bottom, midchannel zone of the river. Principal downstream movement of all species occurred from 2200 to 0400 [PDT]. Fish collections followed an activity pattern that included migration, feeding, and resting periods.

Knowledge of the distribution of migrating fish is important both to fisheries managers and to scientists interested in migratory behavior. From a practical standpoint, knowledge of where fish migrate may allow technology to be developed with minimal impact on that resource. Information on the location of fish during different phases of their life cycle may also provide clues to specific environmental factors that influence their behavior and ultimately affect their survival (Coutant 1986). Migrational characteristics are adapted toward particular life history strategies (Smith 1985); therefore, comparisons of distribution among species or size classes can further our understanding of anadromous fish biology.

Information on the spatial distribution of juvenile salmonid outmigrants in nonimpounded waters of the mainstem Columbia River is limited to studies of 0–age fall chinook salmon, *Oncorhynchus tshawytscha*, by Mains and Smith (1964). Investigations of the distribution of migrating salmonids in other river systems have been directed at determining the behavior of juveniles during movement from spawning or nursery areas. For example, in the Skeena River drainage in Canada, the lateral distribution of outmigrant pink salmon, *O. gorbuscha*, and sockeye salmon, *O. nerka*, was positively correlated with current velocity. In contrast, coho, *O. kisutch*, and chum, *O. keta*, salmon fry were more uniformly distributed across the river (McDonald 1960). Studies with juvenile sockeye salmon in the Newhalen River, AK showed that most fry and smolts were present in the faster midchannel areas and near the surface (Dames and Moore 1982). To our knowledge, no studies have been conducted to quantify and compare the cross-sectional distribution of juvenile salmonids in lotic environments.

Descriptions of habitat selection have been conducted for many salmonid species in small stream systems. Most indicate a general relationship between increased fish size and greater water depth and/or current velocity (Hartman et al. 1967; Lister and Genoe 1970; Everest and Chapman 1972; Wankowski and Thorpe 1979). Whether this relationship applies to the spatial distribution of migrating fish in a large river has not been established.

We report results from field studies conducted in the Hanford Reach of the mid-Columbia River in 1983 and 1984. The Hanford Reach is now the only unimpounded section of the mainstem Columbia River above Bonneville Dam and below the international border (Fig. 1). Our objective was to obtain estimates of the relative cross-sectional distribution of juvenile chinook salmon, sockeye salmon, and steelhead, *O. mykiss*, during their spring and summer outmigration from upriver spawning and nursery areas. These estimates of distribution were needed to assess the potential for fish to pass through a midriver thermal discharge, located downstream from the study site. Capture locations of fish were also

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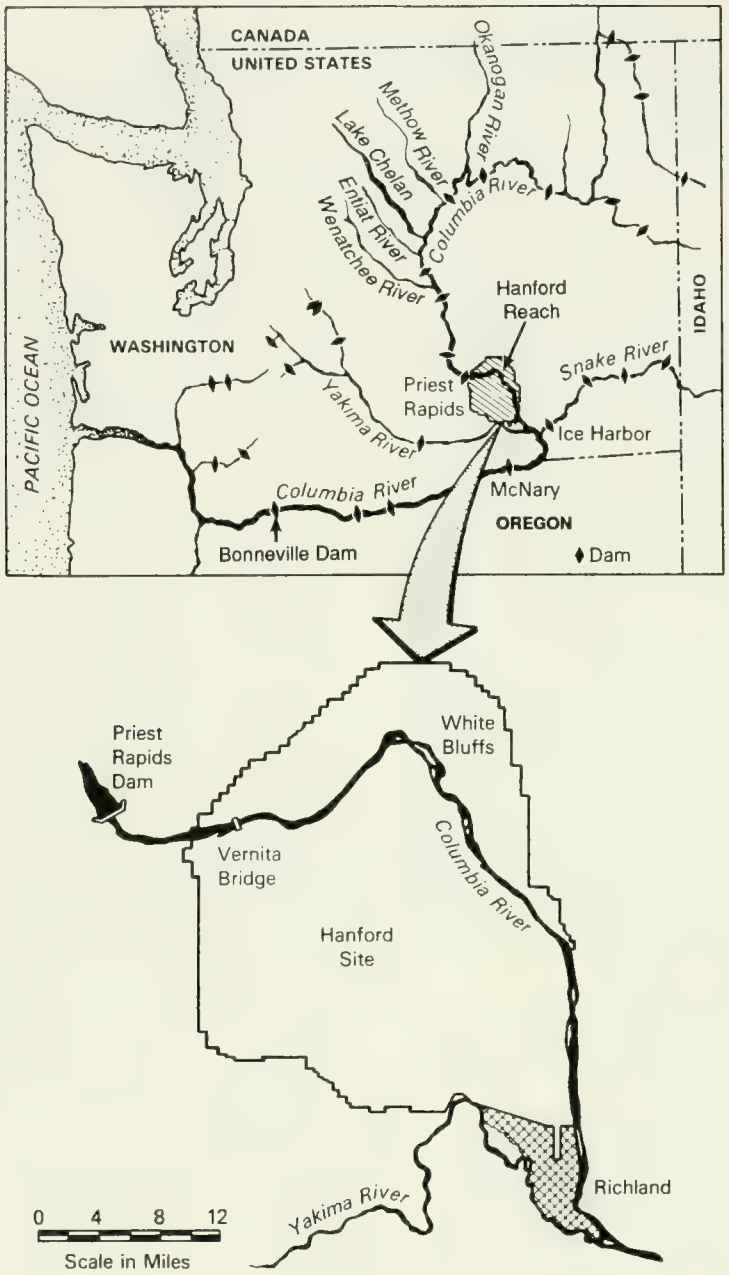

FIGURE 1.—Location of the study area in southeastern Washington.

described in relation to bathymetric and hydrologic characteristics of the river.

STUDY AREA

The Columbia River is about 330 m wide at the study site (river km 613) with average flows of 3,400 m^3/s. The channel is straight, and there are no islands or other major changes in the channel configuration within 6 km of the site. The river bottom slopes gradually from the Benton County side of the river to a distinct channel and rises steeply to the opposite shoreline (Fig. 2). Bottom substrate consists primarily of packed cobble, >10 cm in diameter, and boulders.

River flows in the Hanford Reach are controlled by releases at upriver dams in response to hydroelectric power demand and fish passage requirements. Seasonal flows at the site ranged from 1,220 to 5,270 m^3/s in the summer of 1983 and from 2,600 to 6,330 m^3/s in the spring of 1984. River depths varied by about 4 m as a

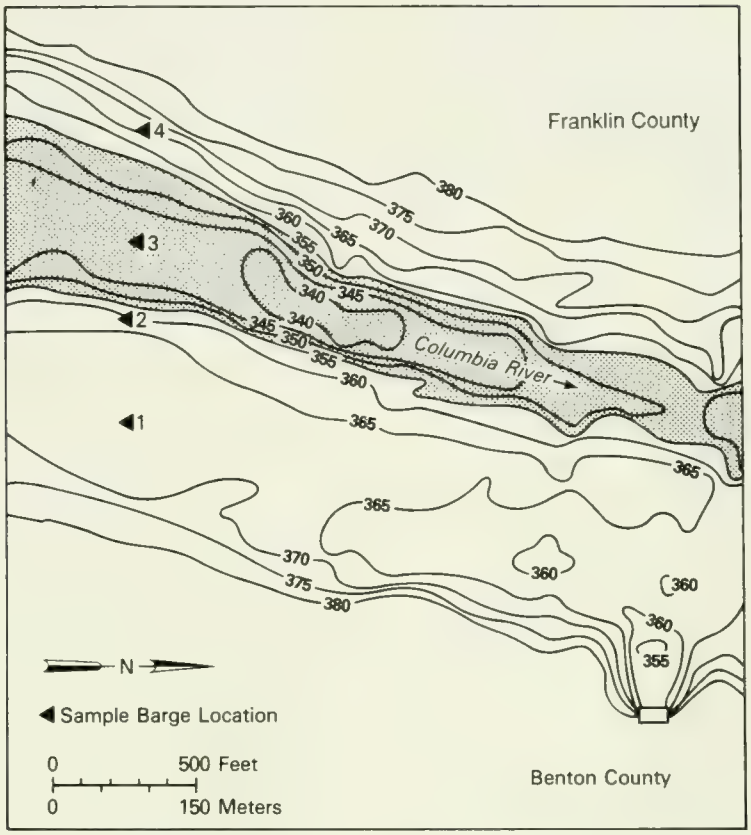

FIGURE 2.—Bathymetry of the Columbia River near the study site, and relative position of barge sampling stations. Contour intervals are river level elevations in feet. The stippled portion shows the midchannel region.

result of this flow pattern. Velocities across the river depended on location, station depth, and river stage (Table 1). Maximum velocities occurred near the river surface. Velocities at midchannel ranged from 0.6 to 2.6 m/s and velocities near the shoreline ranged from 0.1 to 0.5 m/s.

Water temperatures ranged from 18.0°C in August 1983 to 5.2°C in April 1984. Temperatures were uniform across the river until late May; however, from late May through September, daytime water temperatures differed by 2° to 3°C between nearshore and midstream areas because of solar radiation. Visibility (Secchi disc depth) ranged from 142 to 440 cm. Visibility was at a minimum during the late spring freshet and at a maximum in September.

METHODS

Several types of gear were used to provide estimates of fish distribution. Offshore fyke nets mounted on stationary barges were the principal

TABLE 1.—Mean river depth and current velocities at the fyke net sample positions during spring 1984 studies.

Station	Mean depth (m)	Net position	Mean water velocity (m s)
Barge 1	5.5	Surface	0.79
		Middepth	0.67
		Bottom	0.37
Barge 2	6.5	Surface	1.25
		Middepth	1.16
		Bottom	0.98
Barge 3	12.1	Surface	1.59
		Middepth	1.43
		Bottom	1.28
Barge 4	5.9	Surface	0.98
		Middepth	0.79
		Bottom	0.24
Shoreline 1[1]	1.5	Surface	0.18
Shoreline 2[2]	1.6	Surface	0.37

[1]Benton County shoreline.
[2]Grant County shoreline.

collection method because the nets could be simultaneously used at different depths and locations. In 1984, fyke nets were also used near the shoreline to provide comparisons of nearshore abundance. These nets could be moved to accommodate daily fluctuations in river flow. Boat electroshocking and beach seining were also used to monitor nearshore abundance of juvenile salmonids.

Fyke Net Systems

Four steel barges were used as fishing platforms for the offshore fyke nets (barges 1, 2, 3, and 4; see Figure 2). Two barges were permanently anchored at opposite shorelines, one in midstream, and the other in midchannel. The dimensions of the two barges were 4.3 by 8.1 m and two were 4.9 by 9.1 m. The platforms and rigging setup were modified after Mains and Smith (1964). A 13 mm (½-in.) steel cable was used to attach each barge to a 4,500 kg steel anchor (Fig. 3). A drum winch, with a 6 or 8 mm windlass cable, was used to raise and lower the net from the back of the barge. Battery-powered windlass winches (Superwinch, Model EW 600[1]) and hydraulic-powered gypsy hoists (Kolstrand Model 5-24) were used to operate the drum winch on the two shoreline and two midstream stations, respectively. Hand hoists (come-alongs) were used to maintain tension on the windlass cables because the river levels fluctuated daily.

Each barge fyke net had a 1.5 × 1.5 m opening and was 7 m long. The main body tapered uniformly to a 20 cm diameter opening at the cod end. All netting was made of 6 mm (¼ in.), heavy-duty, knotless nylon mesh. The net frame was built from streamlined aircraft tubing, measuring 86 × 36 × 1 mm. A General Oceanics Model 2030 flowmeter was attached to the mouth of the net. In 1984, a detachable net constructed of 5 mm (3/16 in.) heavy-duty, knotless nylon mesh was attached to the nylon sleeve on the cod end to retain smaller fish. This net was 1 m long, 20 cm across, and had a zippered opening for reaching fish and removing debris.

Shoreline fyke nets had a 1 m^2 opening and were 4.5 m long. No wings were used, but an internal fyke was added that decreased the effective mouth size to 0.3 m^2. All netting was made of 5 mm (3/16 in.), heavy-duty, knotless nylon mesh. The mouth or upstream end of the net was rigged with a weight/float line to keep it vertical. A weight/float retrieval line was also attached to the downstream end of the net.

Fyke Net Sampling Design and Procedure

The offshore nets were fished from each of the four barges for five 24 h periods each week from 26 July through 24 September 1983 and from 23 April to 29 June 1984. We also sampled for four days in late July 1984. The spring sampling coincided with the expected maximum abundance of

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

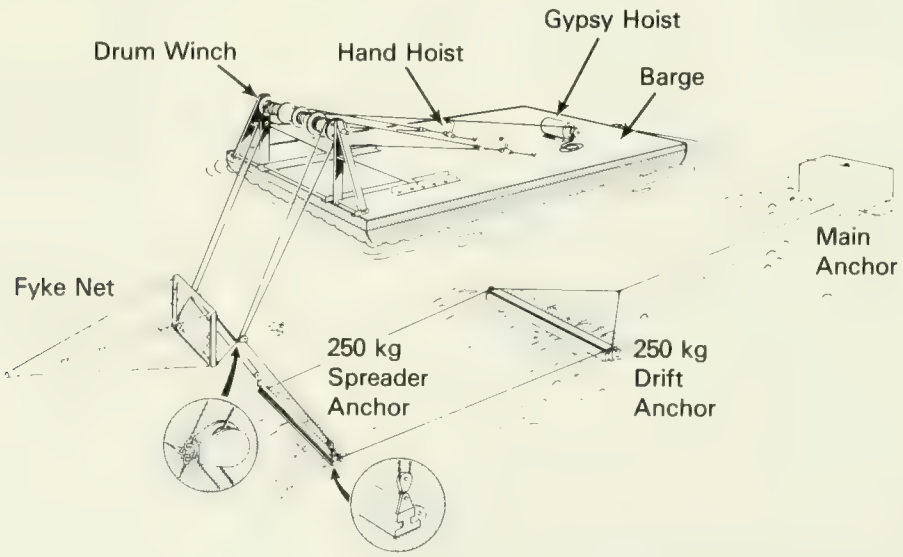

FIGURE 3.—Design of the fyke net rigging and anchoring system.

juvenile fall chinook salmon emerging from the Vernita Bar area (Page et al. 1976) and with the period of greatest catches of juvenile coho, chinook, and sockeye salmon, and steelhead at Priest Rapids Dam (Becker 1985). The late summer sampling corresponded to the period of greatest catches of 0–age fall chinook salmon at Priest Rapids Dam (Raymond 1967; Sims and Miller 1977; Hovland et al. 1982).

Sampling periods within each week were selected by a stratified random process to give equal weight to weekday and weekend intervals. To differentiate between diel variations in migration pattern, each day was divided into four equal time blocks starting at 0400 PDT (i.e., 0400–1000, 1000–1600, 1600–2200, and 2200–0400). The scheme provided one all-dark, one all-light, and two transition (dawn and dusk) periods. All barge stations were fished simultaneously at a predetermined depth. One net set of approximately 2 h duration was taken at each of the surface, mid-, and bottom depths according to a random schedule during each 6 h time block. Water temperature, sample and station depths, duration of set, and flowmeter readings were recorded for each sample. Secchi disc depth was recorded daily at noon. Current velocity measurements were taken at 1 m below the surface, at middepth, at 1 m from the bottom at each of the four stations, and over a range of flows using a Bendix Model Q-15 current meter.

Three people worked each shift. Generally, a net could be raised, checked for catches, cleaned of debris, and lowered to the next sampling depth within 5 minutes. Nets at all four stations would usually be tended and repositioned within 15 to 30 minutes. Some samples were lost because of water levels and high flows. Once, a submerged log hit the midchannel net and broke the spreader anchor cable.

The shoreline fyke nets were used for five 24 h periods each week from 30 April to 29 July 1984. To differentiate between diel variations in catch, each 24 h day was divided into four equal time blocks of 6 hours each. Collection intervals coincided with the four barge fyke net sampling periods. Nets were set parallel to the shoreline and opposite the barges at depths of 1 to 2 m.

Supplemental Sampling Gear

A boat-mounted electroshocker (Smith-Root Type VI Electrofisher), powered by a 240 volt generator, was used to sample nearshore fish populations near the barge stations during 1983 and 1984. Each shoreline station was sampled once per week during each of the four 6 h time blocks when fyke nets were sampled. A single pass with the electroshocker was conducted through each 400 m transect at depths of 1 to 2 m. Stunned fish were collected with dip nets, and all juvenile salmonids were measured and released. Catch per unit effort was based on duration of shock.

Duplicate seine hauls were made at each of four permanent stations near the barges with a 9.1 by 1.2 m net constructed of 3 mm (⅛ in.), heavy-duty, knotless nylon mesh. The stations were sampled once per week during daylight hours from April through June 1984. About 50 m^2 of shoreline were sampled with each set. All salmonids were enumerated and subsamples (usually five fish per station) were retained for measurements.

Data Analysis

Estimates of the proportional distribution of fish groups caught at various stations and depths by fyke net were based on a multinomial distribution of the fish caught among the various combinations of station and depth (Cochran 1977). Relative catch per unit effort (CPUE) was calculated on the basis of unit time/cross-sectional area sampled and on volume sampled. A log-linear model was developed to evaluate proportional distribution estimates of 0-age fall chinook, spring chinook, and sockeye salmon smolts using the CATMOD procedure in SAS (SAS 1985). The model was then used to test for two-way interactions among fish groups, barge location, and sample depths. A binomial test for differences (Mainland et al. 1956) was also used to evaluate patterns of distribution for some species.

RESULTS

Estimates of cross-sectional distribution were different for each of the six groups of juvenile salmonids collected. The differences are described in terms of species, life stage, and migration timing.

Distribution of 0-Age Chinook Salmon

Three groups of 0–age chinook salmon were collected: 1) naturally produced (wild) fish originating from adults spawning in the Hanford Reach above the study site, 2) hatchery fish

from the Priest Rapids Dam rearing facility, and 3) late summer migrant fish from wild stocks that spawn above Priest Rapids Dam or from hatchery releases at Wells Dam. Peak abundance of these three groups occurred at different times (Fig. 4). Juvenile fall chinook salmon originating from the Hanford Reach were collected in higher numbers than any other salmonid group. These fish were already present in the river when sampling began in late April

Spring Outmigration

Wild and hatchery 0–age chinook salmon occurred throughout the river cross section at Hanford, but the highest concentrations occurred at nearshore barge stations (Fig. 5). About 45% of the fish (n = 6,281) were collected at barge 4. In contrast, only 7% of the 0–age chinook salmon were collected in the shoreline nets.

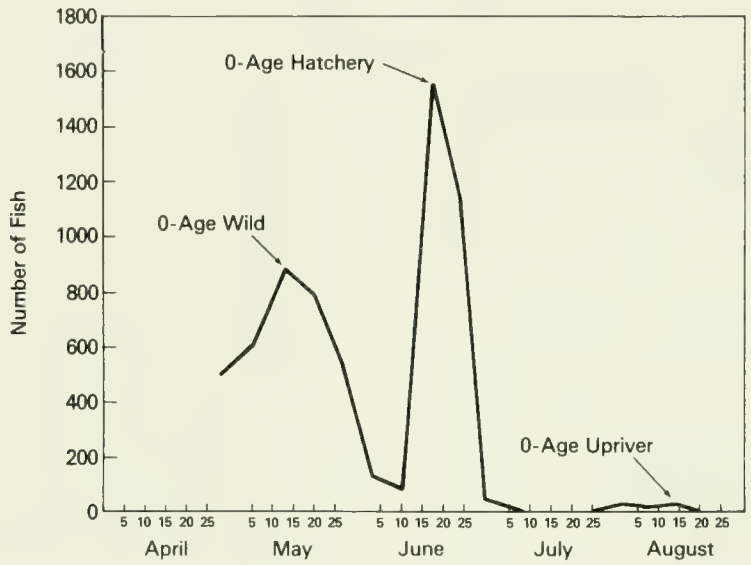

FIGURE 4.—Seasonal patterns of abundance for 0-age chinook salmon populations captured by fyke net near the study site. Sampling effort was uniform throughout the collection period.

1984. Populations peaked in late May, and small numbers were still present in late June when sampling ended. About 60% of the 0–age fall chinook salmon collected in 1984 were wild fish that originated from the Hanford Reach. Hatchery-reared fish appeared in nets within 24 hours of their release from the Priest Rapids rearing facility. These fish differed from wild salmon because of their larger size and deeper body. Most salmonids collected during June were hatchery-released fish. Small numbers of 0-age summer or fall chinook salmon were also collected from July to September 1983 and in July 1984. These fish probably originated in the Wenatchee River, with lesser contributions from the Entiat, Methow, and Okanogan Rivers. Only limited spawning of fall and/or summer chinook salmon occurs in the mainstem Columbia River above Priest Rapids Dam (Horner and Bjornn 1981).

TABLE 2.—Summary of average catch per unit effort for 0-age chinook salmon caught by fyke nets in spring 1984.

Station	Depth	Number/h	Number/$m^3 \times 10^6$
Shoreline 1[1]	Surface	0.3	669.0
Barge 1	Surface	0.4	50.7
	Middepth	0.9	120.8
	Bottom	1.3	199.9
Barge 2	Surface	0.6	50.7
	Middepth	0.4	36.4
	Bottom	0.9	88.6
Barge 3	Surface	1.4	90.4
	Middepth	0.5	33.6
	Bottom	2.2	164.6
Barge 4	Surface	1.7	230.5
	Middepth	2.0	285.7
	Bottom	3.5	829.6
Shoreline 2[2]	Surface	0.2	975.0

[1]Benton County shoreline.
[2]Grant County shoreline.

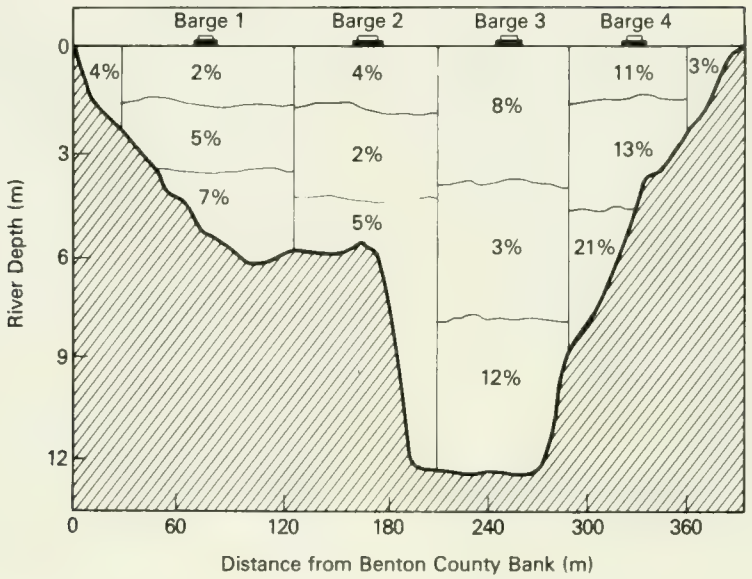

FIGURE 5.—Cross-sectional distribution of 0-age fall chinook salmon (n = 6,281) caught in shoreline and barge fyke nets during spring 1984. Note: horizontal scale is reduced.

Overall, fyke net catches of 0–age chinook salmon ranged from an average of 0.3 fish/h at the Benton County shoreline (shoreline 1), to 3.5 fish/h at barge 4 (Table 2). A peak catch of 152.8 fish/h occurred on June 14 from the bottom depth at barge 4. This quantity corresponded to 5.6 fish/100 m^3 of water filtered through the net. Based on water volume, catch per unit effort was greatest at the Grant County shoreline (shoreline 2).

Little change in fish size was noted for 0–age chinook salmon collected with fyke nets in April and May; 80 to 90% of the fish collected were ≤45 mm fork length (FL) (Fig. 6). However, in June the 0–age chinook salmon collected in the shoreline nets were smaller than those collected in the barge nets. In June, the barge nets collected mainly hatchery fish >80 mm FL, while 60% of the shoreline net totals were wild fish <70 mm FL.

The relative proportion of 0–age chinook salmon caught at the various fyke net stations

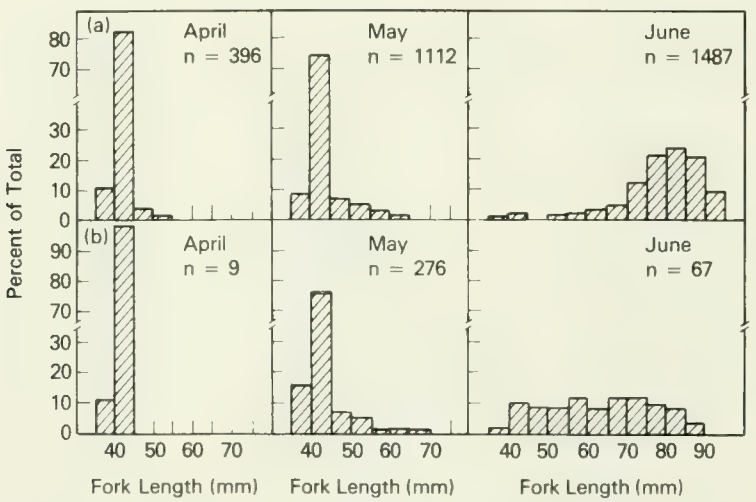

FIGURE 6.—Length-frequency of 0-age fall chinook salmon collected with fyke nets: a) barge sets and b) shoreline sets.

varied seasonally. In general, fish caught in April and May (all wild fish) occurred to a greater extent in shoreline areas where currents were reduced than fish caught in June (~90% hatchery fish). Nearly three times as many 0-age salmon were collected from the two midstream stations (barges 2 and 3) in June than in April and May (Table 3). Analysis of the number of fish caught showed a highly significant interaction ($P \leq 0.0001$) between the April/May and June groups and capture location (barge or depth).

Late-Summer Outmigrants

Low numbers of juvenile fall and summer chinook salmon occurred at Hanford during late summer (July to September). We captured most of these fish (21 of 26) in the midchannel station (barge 3), and 68% of them were collected from the bottom sets. CPUE at barge 3 was 2.2 fish/100 h of sampling (all depths combined). This corresponded to only 1.6 fish/$m^3 \times 10^6$ of water filtered through the nets. CPUE at barge 3 during the peak sampling interval (early August 1983) was 7.1 fish/100 h, or 4.7 fish/$m^3 \times 10^6$ of water filtered through the net.

Distribution of Spring Chinook Salmon Smolts

Yearling-sized chinook salmon occurred throughout the spring in 1984. Most fish originated from the estimated 4 million spring chinook salmon released from upper Columbia River hatcheries in late April.

Catches of yearling chinook salmon were greatest at the midchannel station (73%, n =

TABLE 3.—Estimates of proportional distribution (%) for wild versus hatchery populations of 0-Age fall chinook salmon. Shoreline stations were fished only at ~1 m depth.

Month of capture	Net position	Sample station: Shoreline 1	Barge nets 1	2	3	4	Shoreline 2
April/May	Surface	6.7	3.2	2.1	4.8	14.3	4.5
(n = 3,451)	Middepth	—	7.1	2.0	2.8	9.1	—
	Bottom	—	6.9	2.2	3.2	20.9	—
June	Surface	1.4	1.3	5.7	11.3	6.6	0.8
(n = 2,824)	Middepth	—	2.9	2.9	2.8	5.1	—
	Bottom	—	6.9	8.8	21.9	21.6	—

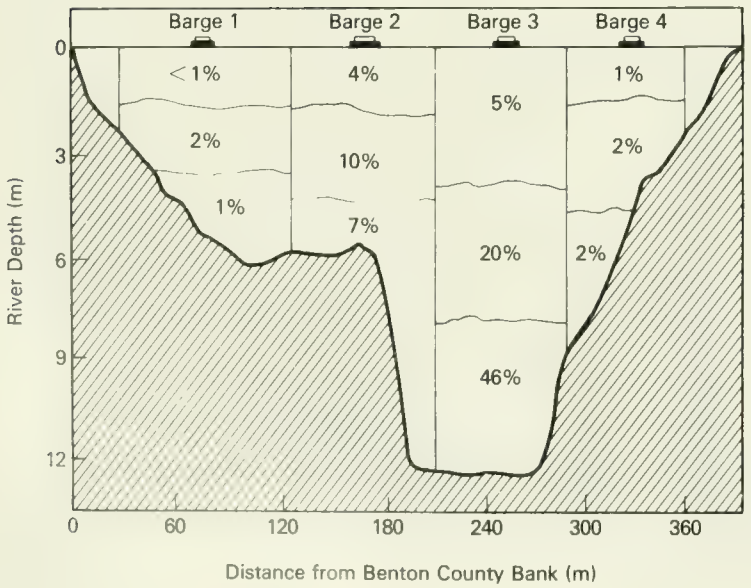

FIGURE 7.—Cross-sectional distribution of yearling chinook salmon (n = 459) caught in shoreline and barge fyke nets during spring 1984. Note: horizontal scale is reduced.

459) (Fig. 7). Catches were low at barges 1 and 4, and no yearling chinook salmon smolts were captured in the shoreline fyke nets. Overall catches were significantly higher ($P \leq 0.01$) from the bottom and middepths at barge 3 than for any other station/depth combination.

The number of spring chinook salmon smolts collected per 100 hours of sampling averaged from 0.3 fish at surface depth (barge 1) to 57.8 fish at bottom depth (barge 3) (Table 4). Although station differences were not as pronounced when CPUE was expressed by volume, the greatest numbers of fish appeared to pass barge 3 in the main river channel.

Spring chinook salmon smolts ranged from 101 to 224 mm FL. Mean size varied little, possibly because most of the fish originated from hatcheries. Scale analysis confirmed that most of the fish (171 of 173) were yearlings.

TABLE 4.—Summary of average catch per unit effort for chinook salmon smolts caught by fyke nets in spring 1984. No smolts No smolts were caught in the shoreline fyke nets.

Station	Depth	Number h $\times 10^2$	Number $m^3 \times 10^6$
Barge 1	Surface	0.3	0.4
	Middepth	2.8	3.7
	Bottom	1.8	2.8
Barge 2	Surface	4.2	3.5
	Middepth	10.4	9.5
	Bottom	7.5	7.8
Barge 3	Surface	6.7	4.5
	Middepth	27.3	18.0
	Bottom	57.8	42.6
Barge 4	Surface	1.3	1.7
	Middepth	2.5	3.6
	Bottom	2.1	5.0

Distribution of Sockeye Salmon Smolts

Juvenile sockeye salmon were the third most abundant salmonid group collected at the site. These fish originated from wild stocks in upper Columbia River tributaries, primarily the Okanogan and Wenatchee River systems (Allen 1977). Peak catches of juvenile sockeye salmon occurred in mid–May 1984.

A total of 173 sockeye salmon smolts was collected at the barge stations, but none were captured by shoreline fyke nets. Most of the sockeye salmon smolts (90%) were caught in midstream areas (barges 2 and 3) from the middepth and bottom sets (Fig. 8). Catch profiles indicated that sockeye salmon smolts migrated at greater depths than other salmonids in 1984. Catches from the bottom depth at barge 3 were significantly greater ($P \leq 0.01$) than catches from any other station/depth combination.

Catch per unit effort for juvenile sockeye salmon averaged from 0.3 to 29.2 fish/100 h of sampling, depending on station and depth (Table

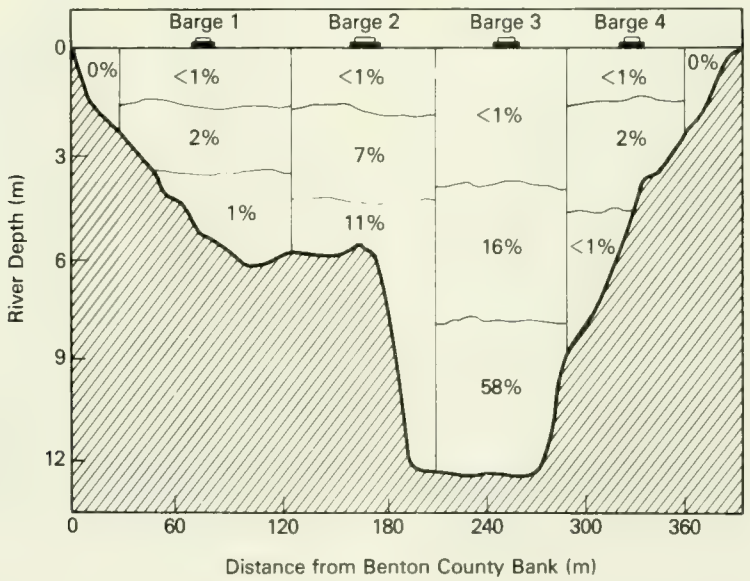

FIGURE 8.—Cross-sectional distribution of sockeye salmon smolts (n = 173) caught in shoreline and barge fyke nets during spring 1984. Note: horizontal scale is reduced.

5). Estimated densities ranged from about 0.2 to 21.6 fish/$m^3 \times 10^6$ of water sampled. Lowest catches were noted for surface sets.

Sockeye salmon were intermediate in size between 0–age fall chinook salmon and spring chinook salmon smolts. Outmigrant sockeye salmon ranged from 74 to 101 mm FL. About 80% of the sockeye salmon were >95 mm FL and, of 96 fish examined, almost all their scales had not yet formed an annulus. Circuli counts for all fish ranged from 8 to 17 and were positively correlated ($R^2 = 0.71$) with fish length.

TABLE 5.—Summary of average catch per unit effort for sockeye salmon smolts caught by fyke nets in spring 1984. No smolts were caught in the shoreline fyke nets.

Station	Depth	Number/h $\times 10^2$	Number/$m^3 \times 10^6$
Barge 1	Surface	0.28	0.35
	Middepth	0.84	1.11
	Bottom	0.59	0.92
Barge 2	Surface	0.26	0.22
	Middepth	2.93	2.67
	Bottom	5.25	5.20
Barge 3	Surface	0.28	0.19
	Middepth	7.25	4.77
	Bottom	29.20	21.64
Barge 4	Surface	0.50	0.67
	Middepth	1.00	1.42
	Bottom	0.26	0.62

Distribution of Steelhead Smolts

Small numbers of juvenile steelhead were collected from late April through early June 1984. Most fish had eroded fins characteristic of hatchery stocks. Various agencies released approximately 1.1 million steelhead smolts into the Columbia River above Priest Rapids Dam in 1984. Almost all juvenile steelhead (34 of 39) were collected in the main river channel (barge 3) and from either the middepth or bottom positions. No steelhead were collected in shoreline fyke nets and only one was collected at a nearshore barge station (barge 4).

An average of 0.3 to 5.4 steelhead were collected/100 h of sampling, depending on the net location (Table 6). Catches were highest from the bottom depth at the midchannel station, where about four fish were collected per $m^3 \times 10^6$ of water sampled.

Size of the juvenile steelhead ranged from 165 to 241 mm FL. Scales of 14 fish were examined: 10 fish were yearlings and 4 were age 2.

Other Salmonids

No juvenile coho salmon were captured, even though about 500,000 juveniles were released about 192 km upriver in May 1984 and some were collected by gatewell dipping at Priest Rapids Dam. One juvenile mountain whitefish, *Prosopium williamsoni*, 77 mm FL, was collected in late May 1984.

Distribution Based on Supplementary Sampling

Chinook salmon were the primary salmonid species collected by electroshocking (Table 7). Numbers of chinook salmon smolts peaked in nearshore areas in early May 1984. Wild 0–age chinook salmon dominated catches in late May, and hatchery-released 0–age chinook salmon dominated in late June. Late-summer migrant chinook salmon smolts were also electroshocked in small numbers from late July to early September 1983. Steelhead comprised 7% of the total (n

TABLE 6.—Summary of average catch per unit effort for steelhead smolts collected by barge fyke nets in spring 1984. No smolts were caught in the shoreline fyke nets.

Station	Depth	Number/h $\times 10^2$	Number/$m^3 \times 10^6$
Barge 1	Surface	0	0
	Middepth	0	0
	Bottom	0	0
Barge 2	Surface	0.26	0.21
	Middepth	0.26	0.24
	Bottom	0.55	0.55
Barge 3	Surface	0	0
	Middepth	2.61	1.72
	Bottom	5.37	3.98
Barge 4	Surface	0	0
	Middepth	0	0
	Bottom	0.26	0.62

TABLE 7.—Seasonal totals for juvenile salmonids caught by boat electroshocker in shoreline transects. Each of two 400 m shoreline transects was sampled four times daily.

Date	Total sample days	Species		
		Chinook salmon	Sockeye salmon	Steelhead
August 1983	4	2	0	0
September 1983	3	4	0	0
April 1984	1	3	0	0
May 1984	5	168	0	3
June 1984	4	191	1	1

= 375) yearling-sized salmonids collected by electroshocking during the spring 1984 studies. Only one juvenile sockeye salmon was collected by boat electroshocking.

Overall, 3,982 0–age chinook salmon and 1 juvenile sockeye salmon were collected by beach seining. Almost all of the chinook salmon captured with seines originated from upstream spawning areas near Vernita Bar. Catches peaked on 17 May with 178 fish/seine haul. Numbers declined in June despite the large numbers of hatchery fish present. The size of 0–age chinook salmon collected with seines (Fig. 9) was similar to those collected with fyke nets in April and May. However, fish collected with barge fyke nets in June (see Figure 5) were generally larger than those collected with seines. No juvenile spring chinook salmon or steelhead were collected with beach seines.

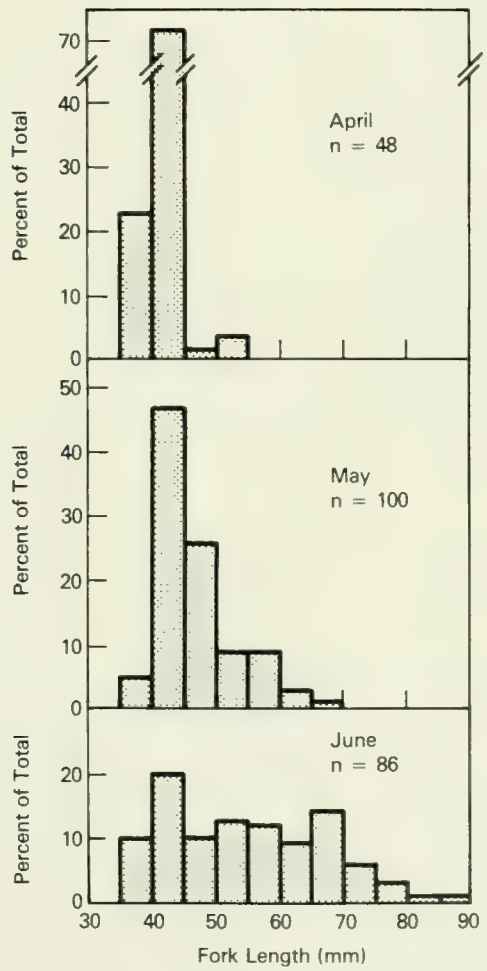

FIGURE 9.—Length-frequency of 0-age fall chinook salmon captured by beach seine in spring 1984.

Diel Patterns In Salmonid Migration

Principal movement of all salmonids occurred between the hours of 2200 and 0400, based on barge fyke net collections; however, differences in peak movement among species were evident from the barge catches (Fig. 10). For example, only 0–age fall chinook salmon (wild and hatchery populations) were collected during daylight hours. For these populations, peak catches occurred just after darkness (2200 to 2400). In contrast, fyke net catches of sockeye salmon, spring chinook salmon, and steelhead smolts peaked between 2400 and 0400. Although nocturnal movement was also evident based on shoreline fyke net catches, a higher proportion (~22%) of the 0–age chinook salmon were collected in shoreline nets during daylight hours (Fig. 11).

Diel patterns of distribution based on electroshock catch totals contrasted among the different groups of chinook salmon (Fig. 12). Peak numbers (55%) of the 0–age fall chinook salmon in April and May were collected from the hours of 1600 to 2200; 44% of the 0–age hatchery fall chinook salmon (June fish) were collected from 0400 to 1000; and 80% of the hatchery spring chinook salmon and late summer migrant chinook salmon were collected during the night from 2200 to 0400.

DISCUSSION

Our studies showed that distributional patterns were different for each of the three most abundant groups of juvenile salmon (i.e., fall chinook, spring chinook, and sockeye salmon). Our hypothesis that fish distribution was independent of barge station and depth was rejected, suggesting that different groups acted differently at different barges and at different depths. Salmonid outmigrants in the Hanford Reach exhibited patterns of proportional distribution that were mainly size related (Table 8). Larger outmigrants (i.e., chinook salmon, sockeye salmon, and steelhead) occurred near the bottom, midchannel zone of the river, while the smaller wild and hatchery 0–age fall chinook salmon preferred the shallower shoreline areas.

The relatively high contribution of fall chinook salmon to the total catch during the spring resulted primarily from the large numbers of wild fish emerging in the Hanford Reach and the hatchery fish released there. About 90% of the salmonids collected were 0–age chinook salmon. Collectively, this group comprised about 70% of

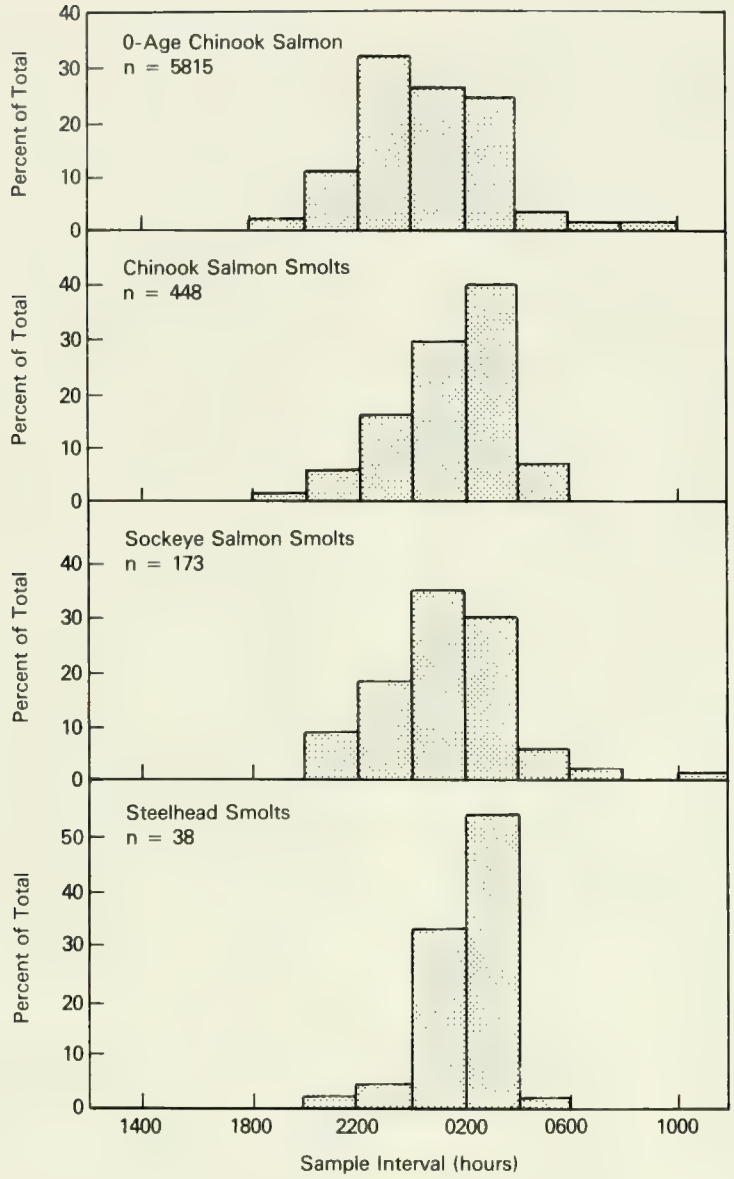

FIGURE 10.—Diel catch patterns of juvenile salmonids collected by barge fyke nets during spring 1984.

the juvenile salmonids estimated to pass the study site in 1984. Wild populations of 0–age fall chinook salmon were more vulnerable to active and passive netting techniques because they were smaller relative to juvenile salmonids produced or released upriver. Because the smaller 0–age fall chinook salmon that emerge from redds at Vernita Bar use the Hanford Reach primarily for temporary feeding and rearing (Becker 1973), their distribution may differ from the distribution of smolts migrating from upstream sites.

The cross-sectional distribution of chinook salmon fry (36 to 70 mm FL) in our collections was similar to that observed by Mains and Smith (1964) for 0–age fall chinook salmon in the Columbia River at river km 550. Although Mains and Smith also reported data from "yearling" outmigrants in June and July, the length (85 to 90 mm FL) of these fish approximated that of later-migrating stocks of 0–age fish from upriver. The spatial distribution described by Mains and Smith for yearlings (based on volume sampled) was nearly identical to the distributions that we obtained for naturally produced stocks of 0–age fall chinook salmon. In both

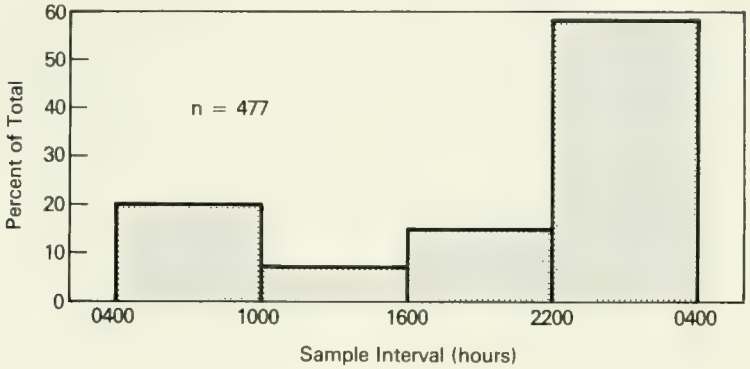

FIGURE 11.—Diel catch patterns of 0-age fall chinook salmon collected by shoreline fyke nets during spring 1984.

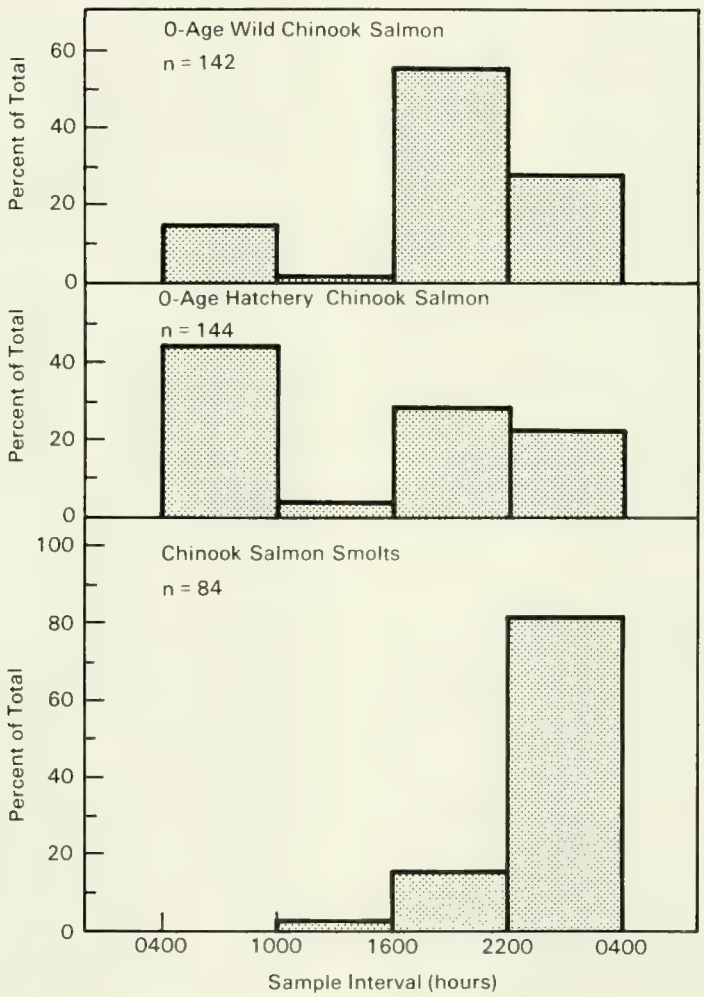

FIGURE 12.—Diel catch patterns of juvenile chinook salmon collected by shoreline electroshocking during spring 1984.

TABLE 8.—Relationship of juvenile salmonid size to fyke net capture location. Key: S1,S2= shoreline stations, B1-B4 = barge stations, s = surface, m = middepth, b = bottom, ns = not sampled.

Population	Mean size (mm)	Depth zone	Proportional distribution (%) S1	B1	B2	B3	B4	S2
Chinook salmon								
0-age fall (wild)	45	s	7	3	2	5	14	3
(*n* = 3,451)		m	ns	7	2	3	19	ns
		b	ns	7	2	2	21	ns
0-age fall (hatchery)	85	s	1	1	6	4	7	1
(*n* = 2,824)		m	ns	3	3	3	5	ns
		b	ns	7	9	22	22	ns
0-age summer migrant	114	s	ns	0	0	9	0	ns
(*n* = 26)		m	ns	0	0	14	5	ns
		b	ns	0	0	73	0	ns
1-age spring	140	s	0	1	4	5	1	0
(*n* = 459)		m	ns	2	10	20	2	ns
		b	ns	1	7	40	2	ns
Sockeye salmon	90	s	0	1	4	5	1	0
(*n* = 173)		m	ns	2	6	16	2	ns
		b	ns	1	11	58	1	ns
Steelhead	200	s	0	0	3	0	0	0
(*n* = 39)		m	ns	0	3	23	0	ns
		b	ns	0	8	62	3	ns

studies, most fish were collected in shoreline areas, but catches from one shoreline were about three times greater than catches from the opposite shoreline. Thus, the physical features of some shorelines appear to influence the distribution of juvenile fall chinook salmon.

Low catches of chinook salmon smolts during the late summer may reflect the small population size in upriver areas. The number of summer and fall chinook salmon spawning above Priest Rapids Dam in 1982 was lower than the 1972–82 10 yr average.[2] The total outmigration of up-river 0–age chinook salmon in 1983 was about 1 million fish (estimate based on escapement of adult summer and fall chinook salmon over Priest Rapids Dam in 1982 and historical production factors), or only 40% of the numbers estimated by Sims and Miller (1977) for the 1976 outmigration. Because the mouth openings of the four barge fyke nets collectively only sample 0.1–0.2% of the river cross section, small sample numbers would be predicted for fish present at low densities.

Species-specific differences in behavior also affected spatial distribution. For example, almost all sockeye salmon smolts were collected from midstream portions of the river. This phenomenon was not entirely consistent with the size-related model of fish distribution noted for the different groups of juvenile chinook salmon. Other studies of lateral distribution have shown that yearling sockeye salmon migrate primarily in midriver, utilizing areas of highest current velocity (Dames and Moore 1982). The apparent preference of juvenile sockeye salmon for the river bottom near our study site also contrasts to that observed for lentic populations, which reportedly migrate primarily near the surface (Johnson and Groot 1963).

Electroshocking and beach seining showed that the shoreline fyke nets could not be used to effectively collect larger juvenile salmonids. Although differences in gear effectiveness make direct comparison of methods impossible (Hulbert 1983), it appears that nearshore estimates of distribution based on shoreline fyke net catches were low. For example, spring salmon and steelhead smolts were sometimes electroshocked at night in nearshore areas ~1 m deep, but none were collected in shoreline fyke nets that were fished at similar depths. Daytime catches in shoreline fyke nets were also low when compared with the observed densities of

[2]Rod Woodin, Washington Department of Fisheries, Olympia, WA 98504, pers. commun. November 1983.

0–age chinook salmon during seining. For some species, active sampling techniques helped support distribution trends observed from fyke net data. For example, the preference of migrating sockeye smolts for offshore areas was also indicated by the absence of sockeye salmon in nearshore collections using electroshocking and seines.

In our study, hatchery-reared 0–age chinook salmon (range 75 to 90 mm FL) were less abundant in shallow nearshore areas than wild stocks. This spatial segregation was evident for both seining and fyke net collections. Thus, differences in distribution patterns that may be attributed to size, season, or physiological condition were also evident.

Diel movement patterns were consistent with those observed in previous studies of migrating juvenile salmonids in the Columbia River. Principal movement of outmigrating juvenile chinook salmon occurred during the night at Priest Rapids Dam (Sims and Miller 1977) and at Byers Landing (Mains and Smith 1964). Smith (1974) collected 91% of primarily 1-age juvenile chinook salmon at night in impounded waters on the Snake River. Sockeye salmon have also shown a preference for nocturnal movement in other river systems (Kerns 1961; Dames and Moore 1982). In general, natural light intensity appears to be the major environmental factor controlling diel migration patterns of salmonid fry (Godin 1982).

The observed patterns of diel behavior may have affected the cross-sectional distribution of the juvenile salmonids. For example, we observed that spring chinook salmon smolts were often abundant just after sunset in shallow nearshore areas (≤30 cm deep) of low current velocity. This inshore appearance may have preceded active or passive downstream movement. Nighttime movement into the current may result from a loss of visual contact with the surroundings (McDonald 1960) or a reduction of rheotactic response (Hoar 1953). Both of these mechanisms could result in passive downstream displacement; however, there were distinct differences in diel timing among the four species collected. These differences suggest that migration is not controlled solely by passive mechanisms.

Documented migration rates of juvenile salmonids in the Columbia River are consistent with activity rhythms that include feeding, quiescent behavior, and active migration. At midstream velocities averaging 1 m/s, a passively drifting fish would travel about 29 km in an 8 h night. Migration rates would be faster with higher current velocities, as occurs during the spring freshet (2–3 m/s), or for actively migrating fish. Most salmonid smolts apparently migrate actively in midchannel for only a few hours daily since reported mean migration rates of juvenile salmon through the Hanford Reach are about 56 km/d (Weitkamp and McEntee 1982). The patterns of distribution that we observed probably provide only a partial description of the interacting behavioral characteristics that increase species survival and efficient use of energy reserves.

ACKNOWLEDGMENTS

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Time Series of Growth in the Genus *Sebastes* from the Northeast Pacific Ocean

George W. Boehlert, Mary M. Yoklavich, and Dudley B. Chelton

ABSTRACT: Marine fish populations respond to their physical and biotic environment in complex ways. While direct studies may discern short-term responses at the individual level, time series are needed to describe or predict the population level response to environmental variation or cycles. The ageing technique presented in this paper extracts historical growth information from otoliths through sectioning and careful measurement in order to establish time series of growth. Otoliths of two long-lived species, *Sebastes pinniger* and *S. diploproa*, were collected off the west coast of North America in 1977–84. Fish ages ranged from 1 to 86 years; corresponding birth dates were as early as 1896. Otolith measurements allow description of growth at ages 1–6 for several decades of this century. Although the technique has certain limitations, significant interannual variability in growth is observed, and its relationship to the species' environment is interpreted. Within species, coherence in growth among age groups was not always evident; first year growth in *S. diploproa* was particularly different from growth in other years. For both species, growth responses to environmental factors were not clear; the dominant signal in the time series appears to be increased growth rates after about 1970. This signal is apparently related to density-dependent factors (most likely prey availability) associated with stocks depleted by fishing pressure.

Long-term changes in marine fish populations can be caused by physical and biotic factors as well as man-induced changes. An important goal of fisheries research is to evaluate the effect of fishing on population levels, and this task is easily accomplished if natural variability is understood. Determining causal relationships and superimposing fishing mortality can lead to predictive capability; indeed, many studies in fisheries oceanography model past changes in fish stocks with the objective of forecasting future trends in populations for purposes of fisheries management. Long-term biological data sets are also valuable for ecosystem research, particularly in evaluating the range of natural variability (Wolfe et al. 1987). Historical catch records have been used to assess long-term changes in marine fish populations or stock sizes, and such data from many decades are available for some Pacific salmonid stocks (Mysak et al. 1982; Rogers 1984), for several North Atlantic fisheries (Cushing 1982), and in the Southern Hemisphere for Tasmanian fish populations (Harris et al. 1988). Changes in species assemblages and biotic interactions in the California Current region have been described on both the decade scale (Loeb et al. 1983; Moser et al. 1987) and the century scale (Soutar and Isaacs 1974).

Long-term time series are developed either from continuous data collection or by the extraction of information stored naturally as a chronographic record. Continuous data collection must occur over generations of biologists; starting a new series may not allow achievement of objectives for 30 or more years, so available time series, which are often collected for other purposes, are used. A classic example of extracting data from a chronographic record is the study of fluctuations in population abundance of *Engraulis mordax*, *Sardinops sagax*, and *Merluccius productus* by Soutar and Isaacs (1974). By enumerating fish scales preserved at different depths in anoxic, varved sediments, they defined natural cycles of abundance of these species over 150 years. This approach has recently been applied by Shackleton (1987). Chronological information is also stored in fish otoliths (Radtke 1984; Campana and Neilson 1985). Estimating age of fishes and using otoliths for back calculation are simple examples of extraction of historical information. In addition, the isotopic composition of otoliths has been used to define past thermal habitats occupied by individual fish (Mulcahy et al. 1979; Radtke 1987) and to identify stocks (Mulligan et al. 1987).

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Because studies on fish growth are generally conducted at a single time, time series on the order of several decades are either rare or absent. Some available time series are often produced from different studies, which may not have used the same techniques for sampling, ageing, or interpretation (Boehlert and Kappenman 1980). Using fish scales and interopercular bones from two flatfish species collected over approximately 15 years, Kreuz et al. (1982) established time series of growth and found that growth was negatively correlated with temperature. Width and length of otoliths can be used to estimate length of fish so that past growth patterns can be estimated with back-calculation techniques on otoliths from older fish. Extreme longevity has been documented in the scorpaenid genus *Sebastes* (Bennett et al. 1982; Leaman and Nagtegaal 1987), and ages in excess of 80 years have been reported for several species (Archibald et al. 1981; Boehlert and Yoklavich 1984; Leaman and Beamish 1984). Thus, otoliths of these species can potentially be used to estimate growth from several decades ago.

In this paper, we describe an otolith-based technique for obtaining a historical time series of growth. We apply this technique to two species, the canary rockfish, *Sebastes pinniger*, and the splitnose rockfish, *S. diploproa*, and describe the resultant time series of growth in light of physical and biological factors.

MATERIALS AND METHODS

Otoliths from *S. pinniger* and *S. diploproa* were collected during rockfish surveys conducted by the Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, in 1977 (Boehlert 1980), 1980 (Boehlert and Yoklavich 1984), and 1983 (Wilson 1985). Collection techniques followed Gunderson and Sample (1980). Our objective was to represent as many years of growth as possible; therefore, otolith selection was based upon age alone, and old fish greatly outweighed their relative abundance in a random sample. Additional otoliths from *S. pinniger*, collected off the central Oregon coast in 1984, were obtained from the Oregon Department of Fisheries and Wildlife.

Technical aspects of our methods, described in Boehlert and Yoklavich (1987), are repeated here for completeness because the original information is not widely available. For otolith sectioning and age determination, we followed Boehlert and Yoklavich (1984). Briefly, otoliths were affixed to cardboard tags, embedded in polyester casting resin, mounted on a diamond lapidary saw, and fed onto a pair of thin diamond blades separated by acetate spacers. Dorsal-ventral sections through the focus and perpendicular to the sulcus, approximately 0.4 mm thick, were removed from the center of the otolith, attached to microscope slides, and ground to eliminate artifacts. Total ages were determined from these sections by identifying the first translucent annulus (winter growth zone) and counting sequential growth zones from the center toward the dorsal edge; dorsal annuli at ages near 8–10 years were followed from the dorsal edge to the interior dorsal quadrant, and subsequent annuli were counted to the internal surface.

Annulus measurements, used as a proxy of annual fish growth, were limited to the first 6 years of growth. This limit was imposed because otolith increments became smaller with increasing age; eventually, linear growth stopped, and the otolith began to thicken (Bennett et al. 1982; Boehlert 1985). Two different techniques for otolith measurement were used. In the faster growing *S. pinniger*, whose otoliths are clearer, measurements were from the focus to the dorsal distal edge of each increment (Fig. 1). In *S. diploproa*, whose otoliths are typically more opaque and whose annual increments are smaller, the focus was difficult to identify; for this species, measurements were from the dorsal to ventral distal edges of increments 1–6.

Data from each fish included sex, fork length, date of collection, location, total age, and widths of the increments measured from the otoliths for ages 1–6. The first increment width was a true reflection of first year growth; subsequent measurements, however, integrated past growth. That is, a large growth increment in year 1 could bias the measurement in years 2–6. To remove this correlation and to provide a measure of growth in each year, our analysis used growth increments (GI(i), where i = 1–6) determined by differencing successive measurements. Thus, growth in a given year was not cumulative and generally did not reflect past growth.

Age was subtracted from the year of collection to determine the year of birth. For each fish, each growth increment (1–6) was associated with a specific "year of growth" in the following manner: Increment 1 represented the year of birth or first year growth, increment 2 represented the following year, and so forth. Data on 6 years of growth were available for each fish with the ex-

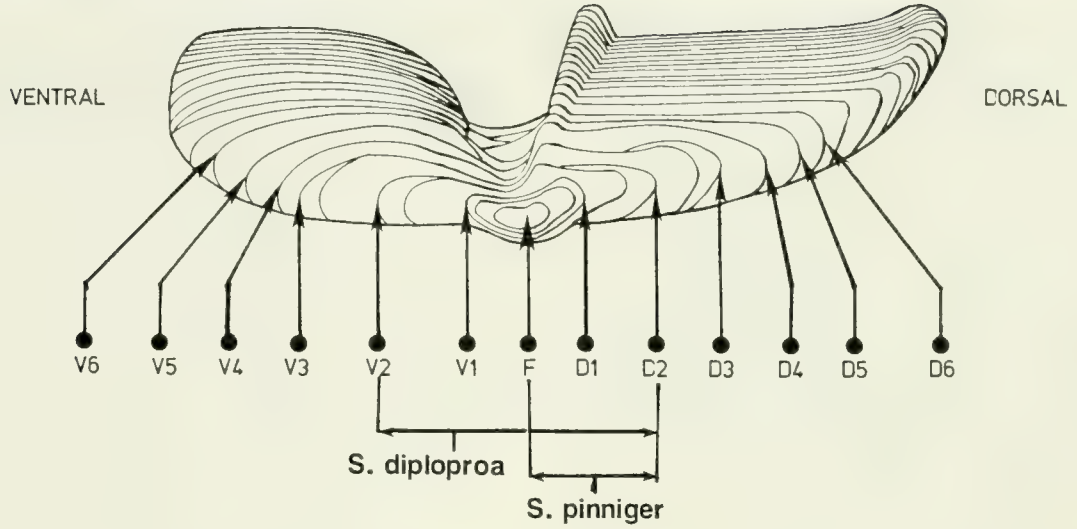

FIGURE 1.—Schematic drawing of an otolith section from *Sebastes* spp. showing the axes of measurements. Measurements for *S. pinniger* were from focus to dorsal distal increment margin (i.e., F to D2); measurements for *S. diploproa* were from dorsal to ventral distal increment margins (i.e., V2 to D2).

ception of those younger than 6 at the time of sampling. As an example, a fish collected in 1980 and aged at 40 years was determined to be born in 1940; therefore, growth measurements from this individual were available for years 1940 (GI(1)) through 1945 (GI(6)).

Most otoliths in our study were from males; otoliths from older females were also included to increase the sample size earlier in the time series. Length at age for these species did not differ between sexes until after sexual maturity, which occurred after age 6 (Boehlert 1980; Boehlert and Kappenman 1980). Still, to test for differences in growth between sexes, we separated the data by sex and then aggregated the data for each GI(i) so that each year of birth had a single, mean value. A paired t-test was used to test for differences in respective growth increments for all years in which both male and female data were available. Growth did not significantly differ between sexes for either species ($P > 0.10$), so data were combined in subsequent analyses.

Certain aspects of the technique, associated with errors in otolith increment measurement and age estimation, may have led to variability in results. From a methodological standpoint, three errors were quickly apparent. First, small changes in the location where the section was removed from the otolith (Fig. 1) may have resulted in slightly different increment measurements; we expected this to introduce relatively minor errors, however, since the sectioning technique (Boehlert and Yoklavich 1984) was designed to be the same. The second source of error occurred in the estimate of total age. Errors in this estimate will result in the assignment of an incorrect year of birth and, thereby, incorrect years of growth for each growth increment; this type of error is probably the most serious, because it will tend to decrease the reliability of real differences between adjacent years. This type of error will increase with increasing age (Boehlert and Yoklavich 1984), and therefore, the reliability of between-year differences in growth will decrease somewhat with increasing age. Finally, errors in selection of annuli (for example, selecting 2–7 instead of 1–6) can occur when making measurements on the section. The cumulative effects of these errors, averaged over many individual samples for each year, should not significantly mask long-term trends in the data. The errors could mask correlations with high frequency environmental features but should not affect correlations with low frequency phenomena.

An additional concern stemmed from the implicit assumption that there is no linkage between longevity and growth; this concept, associated with Lee's phenomenon, is related to size-selective mortality (Ricker 1969). If long-lived individuals are characterized by either faster or slower growth rates during the first 6 years of life than are individuals with shorter lifespans, then we can encounter problems comparing growth of young and old fishes. In lightly

exploited populations of *S. alutus*, for example, very old age groups may have smaller mean lengths than younger age groups, suggesting some type of growth-dependent mortality (Leaman[1]). Markedly smaller mean lengths at age have not been observed, however, for very old specimens of either *S. pinniger* or *S. diploproa* (Boehlert and Yoklavich 1984; Wilson 1985). A genetic basis for differences in growth and age at sexual maturity has been suggested for cod, *Gadus morhua* (Borisov 1979) and brown trout, *Salmo trutta* (Favro et al. 1979). An investigation of the biochemical genetics of *S. diploproa* by using electrophoresis at 29 loci has shown no variation associated with age (L. W. Seeb and G. W. Boehlert unpubl. data). Although negative results cannot rule out a difference, our growth results did not show a consistent trend supporting a genetic basis for growth differences.

Data Analysis and Interpretation

Yearly means of GI(i)'s were calculated and were the values upon which further analysis was made. Standardized growth anomalies (Z-scores) were calculated so that each time series of growth for both species had a mean of zero and a standard deviation of one. This allowed comparison of the growth anomalies in different growth years, standardized for the effects of growth increment magnitude. Comparisons between species were also facilitated by this conversion. A growth anomaly value of zero corresponded to normal growth rate, averaged over the period of the data record.

Within species, there were both similarities and differences between the time series of different age groups. Covariability between different age groups was extracted by principal component analysis (Hotelling 1933) of the six-by-six cross correlation matrix, which expressed interrelationships among the six series of standardized growth anomalies of each species over the period of analysis. The principal component expansion of growth increments can be written as

$$\mathrm{GI}(x,t) = \sum_{n=1}^{6} F_n(x) a_n(t); \qquad (1)$$

where x is the age class (1–6), t is time, and the index n corresponds to component number (1–6). The loadings $F_n(x)$ are the eigenvectors of the cross correlation matrix. The amplitude time series $a_n(t)$ are referred to as the principal components of covariability. The dominant loadings across age groups (those reducing the largest proportions of total variance in the original data set) and the associated principal component time series were interpreted in terms of physical and biological processes influencing growth rate variability. An attempt was made to relate the principal component time series as dimensionless, uncorrelated expressions of growth for each species to time series of environmental and biological data. Environmental data (upwelling, wind speed, and wind stress curl at lat. 45°N, long. 125°W; sea-surface temperature at Neah Bay, WA, lat. 48°22′N) from 1946 to 1977 were provided by the Pacific Fisheries Environmental Group, Monterey, CA. Sea level data from San Francisco (lat. 38°N) were taken from Prager and MacCall[2].

RESULTS

A total of 942 *S. pinniger* (616 males and 326 females) and 802 *S. diploproa* (651 males and 151 females) were used in this study. Specimens of *S. pinniger* ages 2–60 years corresponded with birth dates from 1920 to 1978 (Fig. 2A); *S. diploproa* ages 1–86 years corresponded with birth dates from 1896 to 1979 (Fig. 2B). Total numbers of growth increments measured were 5,600 for *S. pinniger* and 4,714 for *S. diploproa*.

Mean annual size of growth increments for both species showed a reduction with age group, which is typical in fishes. Mean size of increments decreased dramatically (between twofold and threefold) from age groups 1 and 2, then slowly from age groups 2–6 (less than twofold). Growth anomalies for all ages were characterized by significant interannual variability for both species (Figs. 3, 4). The standardized time series for *S. pinniger* (Fig. 3) showed a general, gradual decreasing trend in growth rates for age groups 2–4 from the beginning of the record until about 1965 or 1970. Age group 1 showed a generally decreasing trend prior to about 1957 and an increasing trend thereafter. Age groups 5 and 6 showed a gradually increasing trend virtually

[1]B. M. Leaman, Pacific Biological Station, Nanaimo, B.C., Canada, pers. commun. November 1987.

[2]Prager, M. H., and A. D. MacCall. 1986. An environmental data base describing coastal southern California in the years 1920–1984. Part I: Procedures and summaries. Natl. Mar. Fish. Serv., Southwest Fish. Cent. Adm. Rep. LJ-86-31, 50 p.

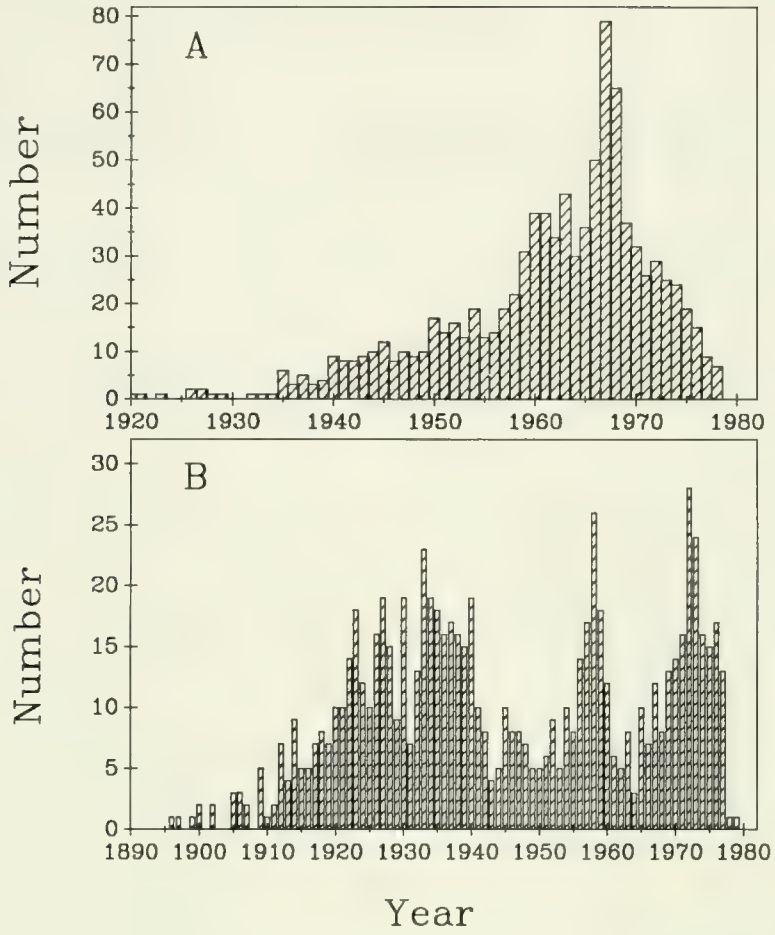

FIGURE 2.—Distribution of the years of birth; males and females are combined. A. *Sebastes pinniger*. B. *S. diploproa*.

throughout the time series. After about 1972, all age groups showed concordance in a relatively abrupt increase in growth rates. This increase may have been shorter lived for age groups 5 and 6, as suggested by the decrease in positive growth rates for the last few years of the record. Positive growth rates continued to increase to the end of the record in the 5 yr running averages for age groups 1–4, though with some significant year-to-year variability in the yearly data.

The time series for *S. diploproa* (Fig. 4) was much longer than for *S. pinniger* (Fig. 3). Age groups 2–4 generally showed a gradual decreasing trend in growth rates prior to about 1965 or 1970. This pattern was similar to that observed for *S. pinniger* age groups 2–4 over the more limited record length. This long-term trend in decreasing growth rates was less evident in *S. diploproa* age groups 1, 5, and 6. Growth rates for age group 5 were nearly normal throughout the record. Growth rates for age group 6 were relatively low in the early part of the record and slightly higher than normal for the period 1930–55. They decreased briefly from 1955 to 1960, then were steady, near-average, or slightly increasing until about 1970. Age groups 2–6 of *S. diploproa* increased in growth rates during the 1970's, coinciding with the high growth rates of all age groups of *S. pinniger* after about 1972. Growth rates for age group 1 of *S. diploproa* were strikingly different from all other age groups of both species of *Sebastes*, with a predominance of variability over much shorter time scales (ca. 5 years) and no evidence of a rapid increase during the 1970's.

The relationship between growth variability in different age groups summarized above from the time series in Figures 3 and 4 were compactly described by the principal components of the six age group time series. We included only years for which yearly mean values of growth were

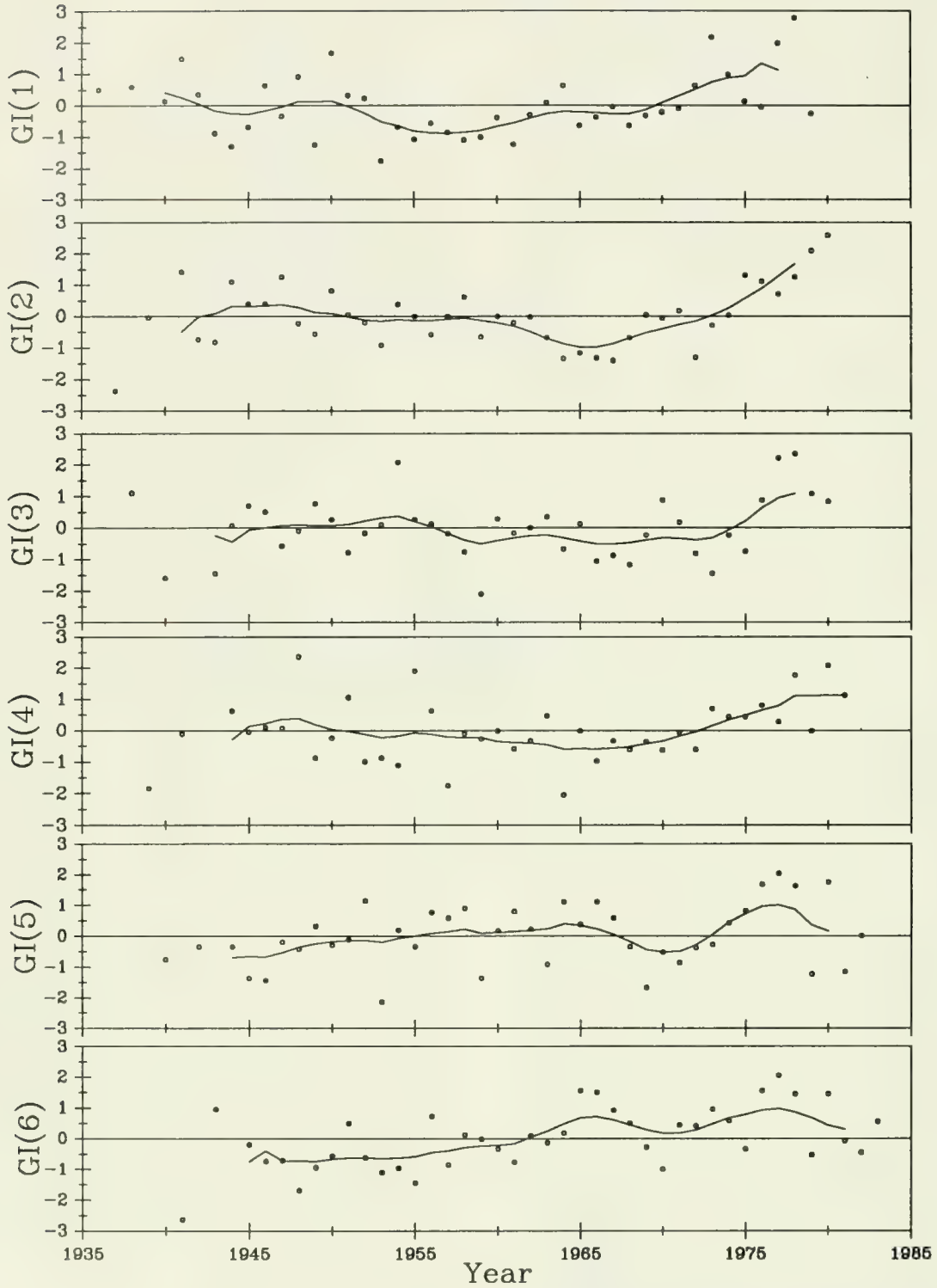

FIGURE 3.—Plot of mean growth anomalies in years of growth 1–6 for *Sebastes pinniger*. Data points represent the yearly mean growth anomalies; the curve represents the double 5-yr running average. Only years with means based upon four or more observations are used.

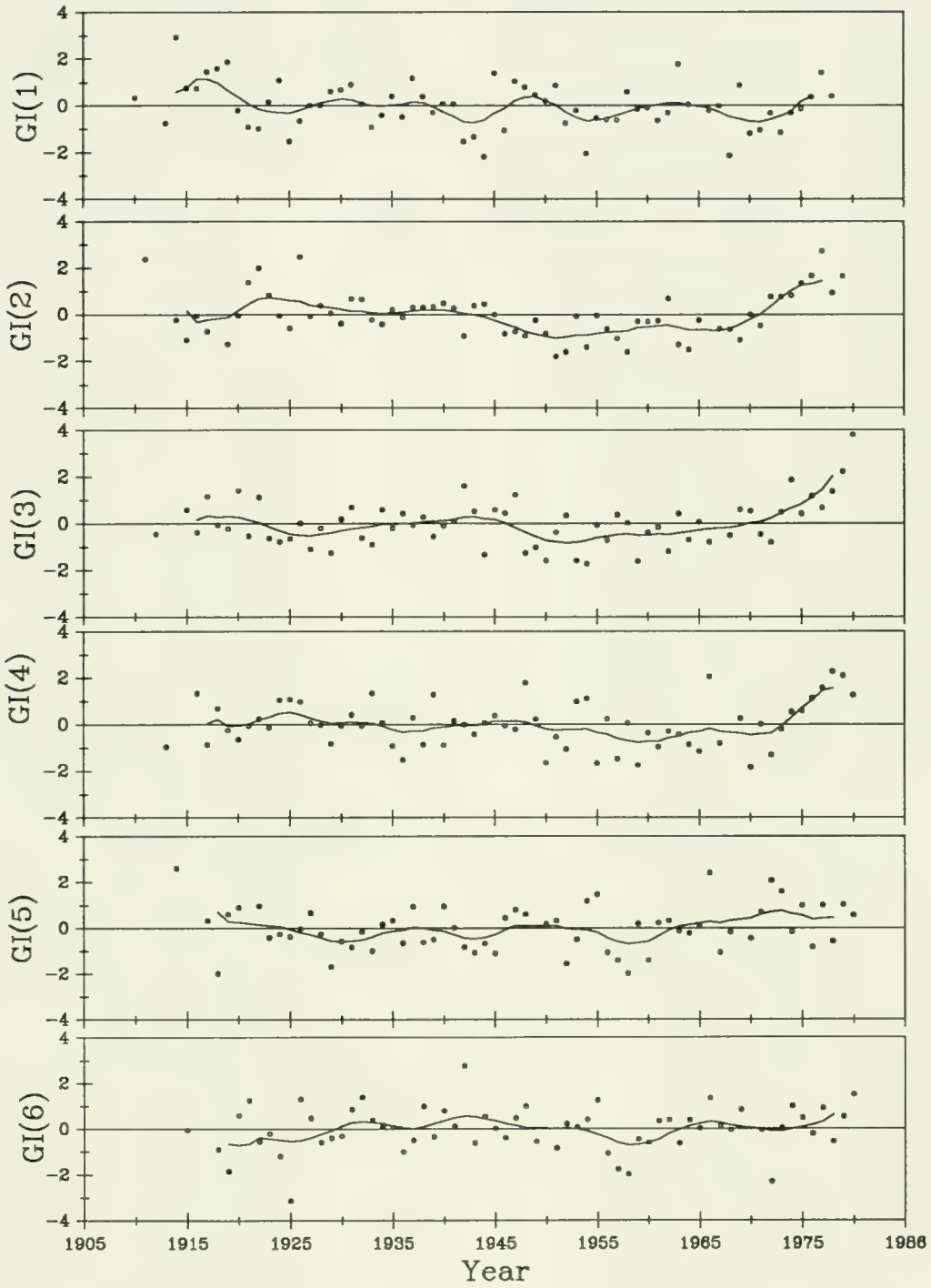

FIGURE 4.—Plot of mean growth anomalies in years of growth 1–6 for *Sebastes diploproa*. Data points represent the yearly mean growth anomalies; the curve represents the double 5-yr running average. Only years with means based upon four or more observations are used.

computed from four or more observations. The first three principal components of *S. pinniger* variability explained 75% of the total variance summed over the six growth anomaly time series; loadings are shown in Figure 5A. Corresponding principal component time series (Fig. 6), or "modes of variability," effectively filter the data to draw attention to the dominant signals discussed above (Fig. 3). By considering the loading values (and thus the relative contribution of each age class) along with the trends in the principal component time series, we described the dominant signals in the time series of the original data. The loadings of the first mode were approximately the same for all six age groups (Fig. 5A); this principal component represented the dominant mode of coherent variability with about the same amplitude in all age groups. The corresponding principal component time series (Fig. 6) is nearly averaged from 1940 to 1970, followed by an abrupt increase beginning about 1972, and represented the high growth rates for all age groups after 1972 (cf. Fig. 3). This was the most pronounced signal in the record, accounting for 36% of the variability over the six age groups.

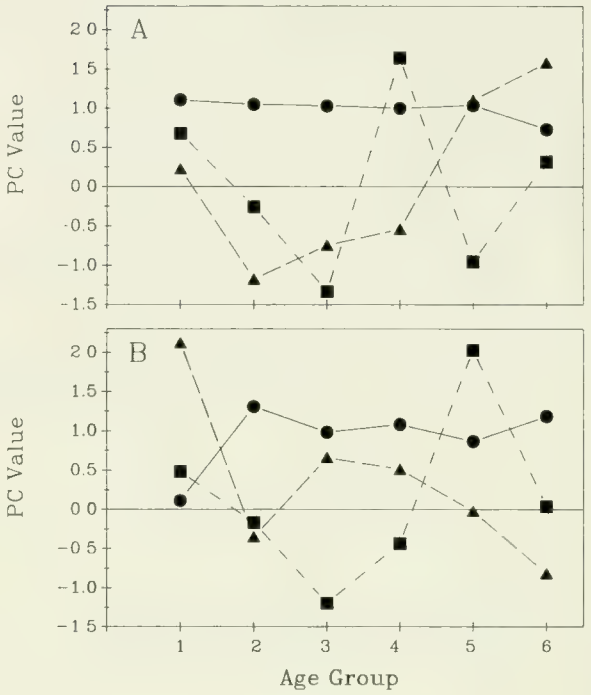

FIGURE 5.—Component (age group) loadings to the three principal components (PC's) explaining the greatest amount of variability in the growth time series. A. *Sebastes pinniger*. B. *S. diploproa*. Circles represent the loadings of the first PC, triangles the second, and squares the third.

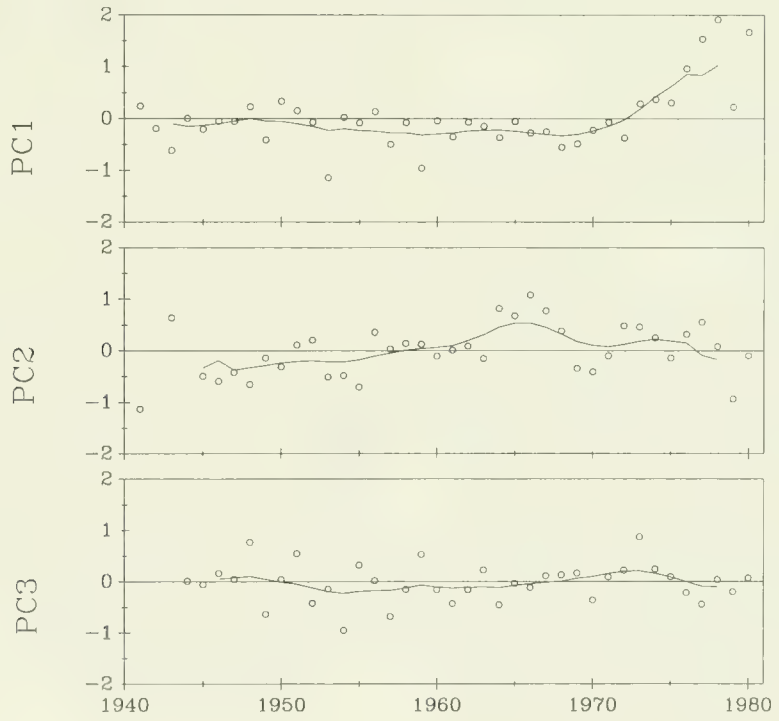

FIGURE 6.—Principal component time series for the three modes explaining 75.0% of the total variance in growth of *Sebastes pinniger* from the six time series in Figure 3. The curve represents the double 5-yr running average.

The second principal component of *S. pinniger* growth variability extracted the coherent trends in the time series evident prior to 1965 (Fig. 3). The loadings (Fig. 5A) were negative for age groups 2–4 and positive for age groups 5 and 6; the loading value for age group 1 was zero, indicating that its variability is not related to this mode. The principal component time series of this second mode of variability (Fig. 6) generally showed a gradually increasing trend from 1945 to 1965, followed by a decreasing trend thereafter. This time variability described well the trends evident in Figure 3 for age groups 5 and 6, for which the loading values (Fig. 5A) were positive. Since the loading values of the second mode were negative for age groups 2–4 (Fig. 5A), this mode of variability (the product of the loading value and the principal component time series, see Equation (1)) corresponded to a gradually decreasing trend in age groups 2–4 growth rates prior to 1965, followed by an increasing trend thereafter. We have no explanation for the difference in the early trends in growth between age groups 5 and 6 and age groups 2–4. Further, growth increments in 1964–68 (Fig. 3) reinforced this difference and produced a peak in the principal component time series in those years (Fig. 6). This second mode of variability describing the trends in growth rates accounts for 24% of the variance in the data.

The loading values of the third principal component of *S. pinniger* growth variability (Fig. 5A) showed no obvious coherent relationship among age groups. The values oscillated from positive to negative among the age groups, and the corresponding principal component time series (Fig. 6) showed no remarkable characteristics. Thus, this mode of variability has no obvious physical interpretation.

The first four principal components of *S. diploproa* variability explained 81% of the total variance summed over the six growth anomaly time series; the loadings for the first three modes are shown (Fig. 5B), with corresponding principal component time series (Fig. 7). The loading values of the first principal component, accounting for 30% of the variance, were approximately the same for age groups 2–6 and zero for age group 1. This highlighted the fundamental difference between growth rate variability in age group 1 and that in the other age groups.

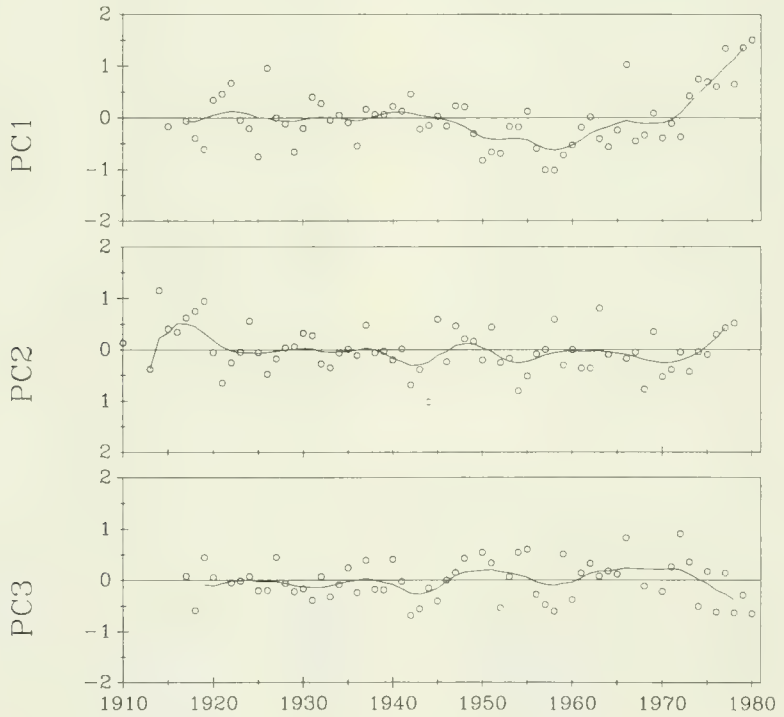

FIGURE 7.—Principal component time series for the three modes explaining 64.6% of the total variance in growth of *Sebastes diploproa* from the six time series in Figure 4. The curve represents the double 5-yr running average.

The principal component time series of this first mode of variability (Fig. 7) showed growth rates as nearly normal in 1915–45, moderately decreasing in 1945–70, and abruptly increasing after about 1972. This was consistent with the earlier interpretation of variability in the individual time series (Fig. 4). The increased growth rates after 1972 coincided with the same signal described by the first principal component of *S. pinniger* growth rates (Fig. 6).

The second principal component of *S. diploproa* growth rates extracted the independent nature of variability in age group 1 and accounted for 19% of the total variance over the six growth anomaly time series. The loading values of this second mode of variability (Fig. 5B) were near zero for all age groups except age group 1. The corresponding principal component time series (Fig. 7) was almost identical to the time series of *S. diploproa* age group 1 (Fig. 4); periods of positive, normal, and negative growth rates in both time series closely corresponded. This further supported the interpretation of this mode of variability as describing age group 1 growth rates. As will be expanded upon in the following section, the lack of linkage between growth rates in age group 1 and the other age groups is likely related to the fact that *S. diploproa* inhabits an environment during the first year of life that is quite different from that during later states of life (Boehlert 1977) and is thus subject to different environmental factors influencing growth rates.

As with *S. pinniger*, the third principal component of *S. diploproa* growth rates has no obvious physical interpretation. The loading values (Fig. 5B) oscillate from positive to negative across the age groups, and the principal component time series (Fig. 7) was nearly normal over the entire record length.

DISCUSSION

The study of growth in marine fishes has typically been concerned with relatively short-term trends in growth of cohorts or populations, most often with fished stocks. Differences in growth may have existed between stocks (Templeman and Squires 1956; Borisov 1979), geographical regions (Boehlert and Kappenman 1980), stock densities, and years (Margetts and Holt 1948; Jones 1983). Such growth differences may be due to genetic factors (Borisov 1979), density dependence (Margetts and Holt 1948; Peterman and Bradford 1987), or environmental factors, most importantly temperature (Brett 1979; Kreuz et al. 1982). The dramatic reduction in stock sizes of many *Sebastes* spp. (Archibald et al. 1983; Ito et al. 1987) has led several authors to suggest density-dependent increases in growth (Gunderson 1977; Boehlert and Kappenman 1980). Recent changes in ageing methodology for *Sebastes* (Boehlert and Yoklavich 1984), however, have rendered long-term comparisons of growth difficult without a historical collection of otoliths.

Analogous to historical time series derived from tree rings (Fritts 1976), the technique described in our paper uses uniform methodology to develop time series of growth for long-lived fishes. Reading of otoliths, however, has more inherent variability than that for tree rings, and the resultant ageing biases described earlier must be considered. The impacts of ageing errors will be most apparent in high frequency signals in the time series and are probably not well resolved by our data; this is the main reason we used the running averages to low-pass filter the data, making the low frequency signals more apparent to the human eye (Figs. 3, 4, 6, 7).

An interesting biological feature of our results is the differing pattern of growth of age group 1 *S. diploproa* (Fig. 4), the only age group not contributing significantly to the variance described by the first principal component for either species. In contrast, first year growth in *S. pinniger* was similar to that in age groups 2–6. *Sebastes pinniger* have a relatively narrow seasonal spawning peak (Westrheim 1975; Gunderson et al. 1980), and pelagic young apparently recruited to their juvenile benthic habitats within about 6 months (Richardson and Laroche 1979). *Sebastes diploproa*, however, seemed to spawn during most months of the year (Snytko 1975), and pelagic prejuveniles were present year-round, at least in the Southern California Bight (Boehlert 1977). Assuming that the first annulus is laid down on a seasonal basis, first year growth was probably quite variable. Further, *S. diploproa* are deepwater (200–500 m) members of this genus, but their first year is spent in surface waters, probably in the upper meter of the water column (Boehlert 1977, 1981); thus, the factors influencing growth in the first year may differ from those affecting growth in subsequent years. Temperature can have an important impact on juvenile rockfish growth (see summary in Boehlert and Yoklavich (1983)), but it may not show coherent cycles be-

tween deep and shallow water over the continental shelf off Oregon (Kruse and Huyer 1983); thus, differences between growth rates for age group 1 and later age groups are not surprising.

The dominant signal apparent in all of the time series of growth, except age group 1 of *S. diploproa* (Figs. 3, 4), and in the first principal component for both species (Figs. 6, 7) was that of increased growth after about 1972. Many of the fish used to calculate the growth anomaly values for this period would have been captured before the age at full recruitment to the fishery, which is 12 years for *S. pinniger* (Wilson 1985) and 14 years for *S. diploproa* (Boehlert 1980). A potential concern with the use of fish younger than the age at full recruitment is that the gear will be selective for larger, faster growing individuals; thus, fish younger than the age at full recruitment might conceivably be characterized by more rapid growth rates, resulting in the increased growth rates observed late in the time series (Figs. 3, 4). If true, then the size of growth increments for fish born in a given year should decrease with time from first recruitment until the age at full recruitment (as is true in Lee's phenomenon). Our samples, however, were taken with sampling gear of much smaller mesh than used in the commercial fishery (Gunderson and Sample 1980). Nonetheless, to test for more rapid growth of younger age fish, we compared the six growth indexes of *S. pinniger* born in 1973–77 and collected in 1980 (N = 41, ages 3–7) with those collected in 1984 (N = 51, ages 7–11). This timespan covered the most rapid increase in growth (Figs. 3, 4). The growth indexes did not significantly differ (paired t-test, $P > 0.10$); this suggests that the size of growth increments did not change as fish born in 1973–77 were collected 4 years closer to the age at full recruitment (1984 versus 1980).

An alternative explanation of increased growth in the 1970's was density dependence. Density-dependent growth has been observed in a variety of fish stocks, generally in association with exploitation (Margetts and Holt 1948) or strong year classes (Jones 1983), and is most evident in immature fish (see summary in Ware (1980)). There is little question that stocks of several *Sebastes* spp. have declined under the influence of fisheries (Gunderson 1984; Bracken 1987; Lenarz 1987; Westrheim 1987). Ito et al. (1987) have suggested that stocks of *S. alutus* off Oregon, Washington, and British Columbia declined from a virgin biomass of about 144,000 metric tons (t) to about 13,500 t in the early 1970's. No direct work documents density-dependent changes in growth in this species, although Gunderson's (1977) model of the stock used increased growth as a compensatory mechanism at low stock density. The best evidence for density-dependent growth changes in the genus is for *S. mentella* (Sorokin et al. 1986). For *S. diploproa*, length frequencies from 1977 (Boehlert 1980) were shifted to much smaller sizes than those from 1961 to 1962 (Alverson et al. 1964); this decrease may have been a result of fishing pressure (Boehlert 1980). Faster growth in the region north of California has been described for this species (Boehlert and Kappenman 1980); density-dependent growth increase (since the major stock reduction occurred in the north) was suggested as one of the factors responsible for the geographical growth differences.

The decrease in stock size of many deepwater *Sebastes* spp. along the west coast of North America and the Gulf of Alaska may be related to the growth increase after about 1972 for both species. The major removals of this group by foreign fisheries occurred in the mid-1960's to 1970's (Bracken 1987; Ito et al. 1987; Westrheim 1987). Time series of reliable biomass estimates for *S. pinniger* and *S. diploproa* are not available, but estimates for *S. alutus* have been made using the stock reduction analysis method (Ito et al. 1987). All three species inhabit similar environments and depend upon similar food resources, so biomass estimates for *S. alutus* can be used as a proxy of biomass for the other two species. A comparison of the first principal component time series of *S. pinniger* and *S. diploproa* with the stock size of *S. alutus* on the west coast (Ito et al. 1987) shows that the increase in growth begins slightly after the major stock decline (Fig. 8). The stock size of *S. alutus* is negatively correlated with the first principal component (and thus growth indexes) for both species ($P < 0.01$).

If decreased stock size is responsible for the increased growth evident in both species, it apparently occurs in age groups 1–6 for *S. pinniger* (Figs. 3, 5A) and in age groups 2–6 for *S. diploproa* (Figs. 4, 5B). The ecological differences between age group 1 and older *S. diploproa* (described above) may explain why density-dependent growth does not occur in the young fish. Density-dependent growth in the first year of life has been described for several fishes (van der Veer 1986; Peterman and Bradford 1987) that

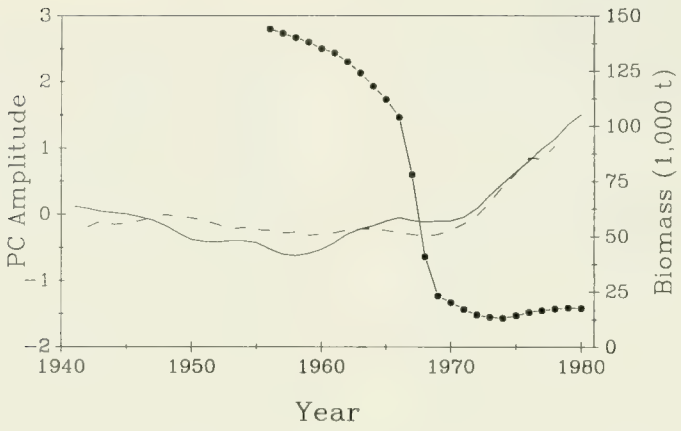

FIGURE 8.—Comparison of the smoothed first principal component time series of *Sebastes pinniger* (dashed line) and *S. diploproa* (solid line) with data on the stock size of *S. alutus* (circles) from Oregon, Washington, and British Columbia (Ito et al. 1987).

typically have a limiting juvenile habitat (often estuarine) and a much more extensive adult habitat. Indeed, Peterman and Bradford (1987) have suggested that density-dependent growth of English sole, *Parophrys vetulus*, off the coast of Oregon occurs only in the first year of life but not later. In *S. diploproa*, the opposite occurs. The adult habitat is restricted bathymetrically and latitudinally, whereas the pelagic prejuveniles occur in a very extensive epipelagic habitat subject to different environmental factors, competitors, and food resources. It is doubtful that variations in density of *Sebastes* in this habitat would impact growth significantly. In the adult habitat of both *S. pinniger* and *S. diploproa*, however, the immense virgin biomass of members of this genus has been reduced significantly. Further, most rockfish species commercially exploited by the trawl fishery rely on the same food resource, with euphausids as the principal prey (Phillips 1964; Brodeur and Pearcy 1984). The increased availability of prey resources associated with stock decline could conceivably result in increased growth in most species. Snytko and Fedorov (1974) suggested that some rockfish species have increased their geographic ranges at the expense of the decreased stocks of *S. alutus*; density-dependent growth could be a corollary of such a range extension.

The nonstationary characteristic due to the sudden increases in growth late in the time series makes correlations of growth indexes with environmental factors difficult to evaluate. Further, sea level, wind stress curl, and the first principal component time series of *S. diploproa* and *S. pinniger* were all serially correlated in the 1946–77 data base, indicating temporal trends that decrease the number of independent degrees of freedom in the sample correlation estimates and that introduce potentially spurious correlations (Chelton 1983, 1984; Bakun 1985). Correlations of the relationship of growth data to time series of physical factors (sea level, sea-surface temperature, upwelling index, and wind stress curl) were determined (Table 1); the 95% significance levels were calculated using the formula in Chelton (1983), which accounts for the reduced number of degrees of freedom from serial correlations. For *S. pinniger*, a significant, positive correlation existed between the second principal component and both the April-September upwelling index and sea level (Table 1); a significant, positive correlation also existed between both growth for age group 6 (G6 in Table 1) and the second principal component with the April-September upwelling index for the prior year. Growth in age group 6 contributed significantly to the variance described by the second principal component (Fig. 5A), so the similarity was not surprising. Feeding by *S. pinniger* increased during the spring-summer upwelling period when *Euphausia pacifica* was the dominant diet item and the frequency of empty stomachs was lower (Brodeur and Pearcy 1984). This must also be the time that fat deposition occurs in this species since the peak fat content was in fall (Guillemot et al. 1985). The effects of upwelling in a prior year on growth may be related to delayed growth using the energy from stored fat reserves built up during

the prior upwelling season. The importance of upwelling in rockfish feeding is shown by the decreased fat storage in El Niño years in *S. flavidus* (Lenarz and Echeverria 1986).

For *S. diploproa*, wind stress curl was negatively correlated with the growth indexes for age groups 2, 4, and 6, with mean growth for age groups 2–6 (G26), and with the first principal component (Table 1), which reflects most closely growth from ages 2–6 (Fig. 5B). Negative wind stress curl is associated with offshore convergence (Nelson 1977), which could concentrate prey (such as euphausids) and potentially increase feeding efficiency during the spring-summer upwelling season when maximum feeding takes place. Sea-surface temperature is negatively correlated with growth in year 2, whereas it is positively (but nonsignificantly) correlated with growth in year 1; the correlation between the second principal component (which reflects growth in year 1) and sea-surface temperature is significant, however, suggesting a real difference between the response of these age groups to temperature. This difference may be involved with an ontogenetic shift in the temperature for optimum growth for this species as noted by Boehlert (1981).

With the exception of the correlations noted above, the general lack of strong relationships of fish growth with physical parameters may be due to several causes. First, errors in methodology may cause lower resolution in the growth time series than would be necessary to demonstrate the associations. Second, the complexity of factors having an impact upon fish growth (Weatherley 1976; Brett 1979) makes detecting relationships of growth with individual physical factors difficult; furthermore, fish growth may be related to environmental factors in a nonlinear fashion. Higher resolution in the measuring technique and minimization of ageing errors will be necessary to address the first of these problems. The second problem can be addressed through nonlinear analysis of the relationships and continuation of the time series of growth anomalies, which will help define the relationships of growth with physical and biological factors.

TABLE 1.—Pearson correlation matrices for six age group growth indexes (G1–6), mean growth indexes (G for *Sebastes pinniger*, G26 for *S. diploproa*), and principal component time series of the three dominant modes of variability (PC 1–3) with environmental factors from 1946 to 1977; mean yearly values (as opposed to smoothed values) are used in these calculations. The mean growth index for *S. diploproa* is for ages 2–6 because of differences in growth in age group 1. The significance levels of coefficients were calculated following Chelton (1983). CURL, wind stress curl at lat. 45°N, long. 125°W; UP, yearly average Bakun upwelling index at lat. 45°N; SSTNB, sea-surface temperature at Neah Bay, WA; UP49, upwelling index averaged for April–September; and SLSF, sea level at San Francisco.

Index	CURL	UP	SSTNB	UP49	SLSF
S. pinniger					
G1	−0.288	0.105	−0.254	0.163	−0.033
G2	0.065	−0.057	−0.032	−0.165	−0.236
G3	0.049	−0.296	−0.078	−0.261	−0.344
G4	−0.058	0.205	−0.173	−0.013	−0.182
G5	−0.066	0.162	−0.140	0.344	0.083
G6	−0.500	0.123	−0.088	0.274	0.429
G	−0.262	0.085	−0.243	0.127	−0.069
PC 1	−0.228	0.077	−0.247	0.109	−0.113
PC 2	−0.344	0.192	−0.061	0.416*	0.459*
PC 3	−0.178	0.261	−0.091	0.081	0.089
S. diploproa					
G1	0.007	0.034	0.363	−0.079	0.075
G2	−0.567*	−0.122	−0.351*	−0.025	−0.041
G3	−0.270	0.127	−0.072	0.062	0.277
G4	−0.453*	−0.392*	0.267	−0.326	−0.140
G5	−0.310	−0.024	−0.293	0.200	−0.216
G6	−0.349*	−0.056	−0.094	0.021	−0.350
G26	−0.619*	−0.163	−0.148	−0.027	−0.120
PC 1	−0.635*	−0.172	−0.145	−0.044	−0.130
PC 2	0.032	0.016	0.438*	−0.126	0.229
PC 3	−0.092	0.029	−0.175	0.200	−0.239

* = $P < 0.05$.

CONCLUSION

The research we describe develops a new technique for constructing historical time series of fish growth and conducts analysis into the causes of growth variation in *Sebastes diploproa* and *S. pinniger*. The technique is applicable to a variety of marine organisms for which chronographic records are deposited in some calcareous structures. Our analysis of the record for *S. diploproa* and *S. pinniger* is characterized by a strong signal of increased growth late in the record. Although this signal is confounded by questions associated with size-selective mortality and Lee's phenomenon, we interpret it to indicate a density-dependent response to stocks depleted by overfishing. Our interpretation can be tested; if stocks of *Sebastes* are allowed to rebuild, the dominant signal of increased growth evident in the time series (Figs. 3, 4, 6, 7) should return to more normal values. We recommend that these time series be continued and that the techniques be applied to other species. The interrelationships among species and further investigation of the role of environmental factors in annual fish

growth variation could provide valuable insights into population responses of fishes to their physical and biological environment.

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Interannual Trends in Pacific Cod, *Gadus macrocephalus*, Predation on Three Commercially Important Crab Species in the Eastern Bering Sea

Patricia A. Livingston

ABSTRACT: Pacific cod, *Gadus macrocephalus*, food habits data from 1981, 1984, and 1985 in the eastern Bering Sea were analyzed to determine interannual trends in consumption of three commercially important species of crabs: the red king crab, *Paralithodes camtschatica*, and two species of snow crabs, *Chionoecetes bairdi* and *C. opilio*. Soft-shell female red king crab were consumed during spring in Bristol Bay. Estimates of percentages of female red king crab standing stock consumed by the Pacific cod population were 3.8%, 2.8% and 1.4% in the respective sampling years of 1981, 1984, and 1985. This implied that Pacific cod were not the major force behind the observed decline in numbers of female red king crab in the population from 1981 to 1985. Predation mortality of *C. bairdi* by cod was estimated to be about 84%, 95%, and 94% of the population of age 1 crab during 1981, 1984, and 1985, respectively. Annual predation removal of age 1 *C. opilio* was 28%, 57%, and 27%, respectively, of the reconstructed population numbers of age 1 crab in the 3 years sampled. Although these calculations indicated that cod may consume large proportions of the age 1 snow crab populations, the estimates are tentative partly because of uncertainties in reconstructing the population numbers of age 1 crab.

The results also indicate that *C. bairdi* are more vulnerable to cod predation because of their high spatial overlap with cod populations, whereas an unknown fraction of the *C. opilio* juvenile population is north of the main survey area and does not overlap with cod. Results from this study suggest that predation by cod may be an important factor influencing survival of ages 1 and 2 snow crab in the eastern Bering Sea.

Pacific cod, *Gadus macrocephalus*, biomass in the eastern Bering Sea has increased by about 800,000 t over the last decade primarily because of two strong year classes spawned in 1978 and 1979. Stock biomass levels have been about 1 million metric tons since 1982 and a growing domestic fishery for this species is responsible for most of the catch (Thompson and Shimada 1987). Because Pacific cod are documented predators of soft-shell red king crab, *Paralithodes camtschatica*, and juvenile snow crab, *Chionoecetes opilio* and *C. bairdi*, (Mito 1974; Feder 1977; Jewett 1978; Blau 1986; Livingston et al. 1986), there has been an increase in speculation linking the decline of crab stocks with the increase in Pacific cod population size. The eastern Bering Sea red king crab population has decreased by an order of magnitude from a maximum of 365 million crab in 1977. Otto (1986) suggested reasons for the decline including weak year class production and large increases in natural mortality, which might be attributed to predation by Pacific cod, disease, or incidental catch in trawl fisheries. Pacific cod may also be implicated in the decline of red king crab abundance in the Kodiak region of the Gulf of Alaska (Blau 1986) and in the disappearance of certain year classes of *C. opilio* snow crab in the eastern Bering Sea (Incze and Schumacher 1986). Although circumstantial evidence has implicated Pacific cod predation in these crab population declines, direct evidence is so far lacking.

The regulation of prey population size by a predator requires that prey mortality rate increase with prey population size (direct density-dependent mortality, Holling 1959). Thus examination of changes in Pacific cod diet with changes in crab population abundance is necessary to determine whether the rate of cod predation on crab changes when crab abundance changes. Total removals of crab by cod need to be estimated and compared with crab population size. If percentage of removal of crab by cod alters with changes in crab density, then cod predation is a likely density-dependent factor regulating crab population size.

I examined the interannual trends in Pacific cod predation on three commercially important crab species in the estern Bering Sea: red king crab, *C. opilio*, and *C. bairdi*. Three years of Pacific cod food habits data from 1981, 1984, and 1985 were analyzed to determine 1) the areas

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where crab predation occurred, and whether this changed with time in response to environmental variables; 2) changes in the percentage by weight and size distribution of crab in the diet by year; and 3) total amounts of crab consumed by the Pacific cod population for each year calculated from food habits data, daily ration, and Pacific cod population abundance estimates. Estimated removals of crab by Pacific cod for each year were compared with the size distribution and population levels of crab estimated from annual research surveys to determine whether cod exerted density-dependent control over crab population size.

METHODS

Sample Collection and Laboratory Analysis

Stomachs were collected from 4,023 Pacific cod (30–107 cm fork length (FL)) during the three years (1981, 1984, and 1985) in the eastern Bering Sea (Fig. 1, Table 1). Samples were taken from May through September using bottom trawl gear on research and commercial fishing vessels. Sampling occurred throughout the 24 h day in 1984 and 1985 and from 0600 to 2000 Alaska daylight time in 1981. Stomachs were removed at sea and placed in cloth bags labelled with information regarding the location of capture and the length, sex, and sexual maturity of the fish. Individual fish weights were calculated using a length-weight relationship developed for Pacific cod in the eastern Bering Sea (Bakkala et al. 1986). Fish showing evidence of regurgitation (i.e., food in the mouth or throat, or a flaccid stomach) were not included in the sample. Stomachs were preserved in 10% formalin and later transferred to 70% ethyl alcohol. Contents were identified to the lowest taxonomic level possible and enumerated. Wet weights were recorded after the contents were blotted with paper towels. If carapaces were intact, snow crabs in the stomachs were measured to the nearest millimeter carapace width (CW), and king crabs were measured to the nearest millimeter carapace length (CL).

Data Analysis

Pacific cod were divided into two size groups for data analysis: 30–59 cm FL and ≥60 cm FL. Previous studies (Livingston et al. 1986) show that cod become increasingly piscivorous beyond 60 cm FL, and mean stomach content weight as a percentage of body weight is also much larger for cod ≥60 cm in length. Thus, the food habits and daily ration need to be examined separately for the two size groups of cod.

Logistic regression, using the BMDPLR routine in the BMDP statistical software package (Dixon 1983), was performed to determine which major factors (predator size and year) were important in describing variation in predation by cod on a particular crab species. The dependent variable was the presence or absence of a crab species in cod stomachs from two cod size groups (Size 1 = 30–59 cm, Size 2 = ≥60 cm) during the three sampling years (1981, 1984, and 1985). The most parsimonious model was chosen for describing predation on each crab species using the criteria that 1) only factors that resulted in a significant improvement ($P < 0.05$) in model fit be added and, 2) the overall model goodness of fit chi-square be nonsignificant ($P > 0.05$), indicating that the model provided a good fit to the data. In addition, BMDPLR permitted

TABLE 1.—Stomach sample collection information of Pacific cod taken in 1981, 1984, and 1985 in the eastern Bering Sea.

Year	Sampling dates	Number of hauls	Sampling times (ADT)[1]	Number of stomachs			Sampling platform
				30–59 cm	≥60 cm	Total	
1981	5/23–8/3	145	0600-2000	1,130	527	1,657	research vessels
1984	5/9–9/29	157	0000-2359	560	410	970	research vessels foreign commercial vessels
1985	5/5–9/30	148	0000-2359	870	706	1,576	research vessels foreign commercial vessels

[1]ADT is Alaska daylight time.

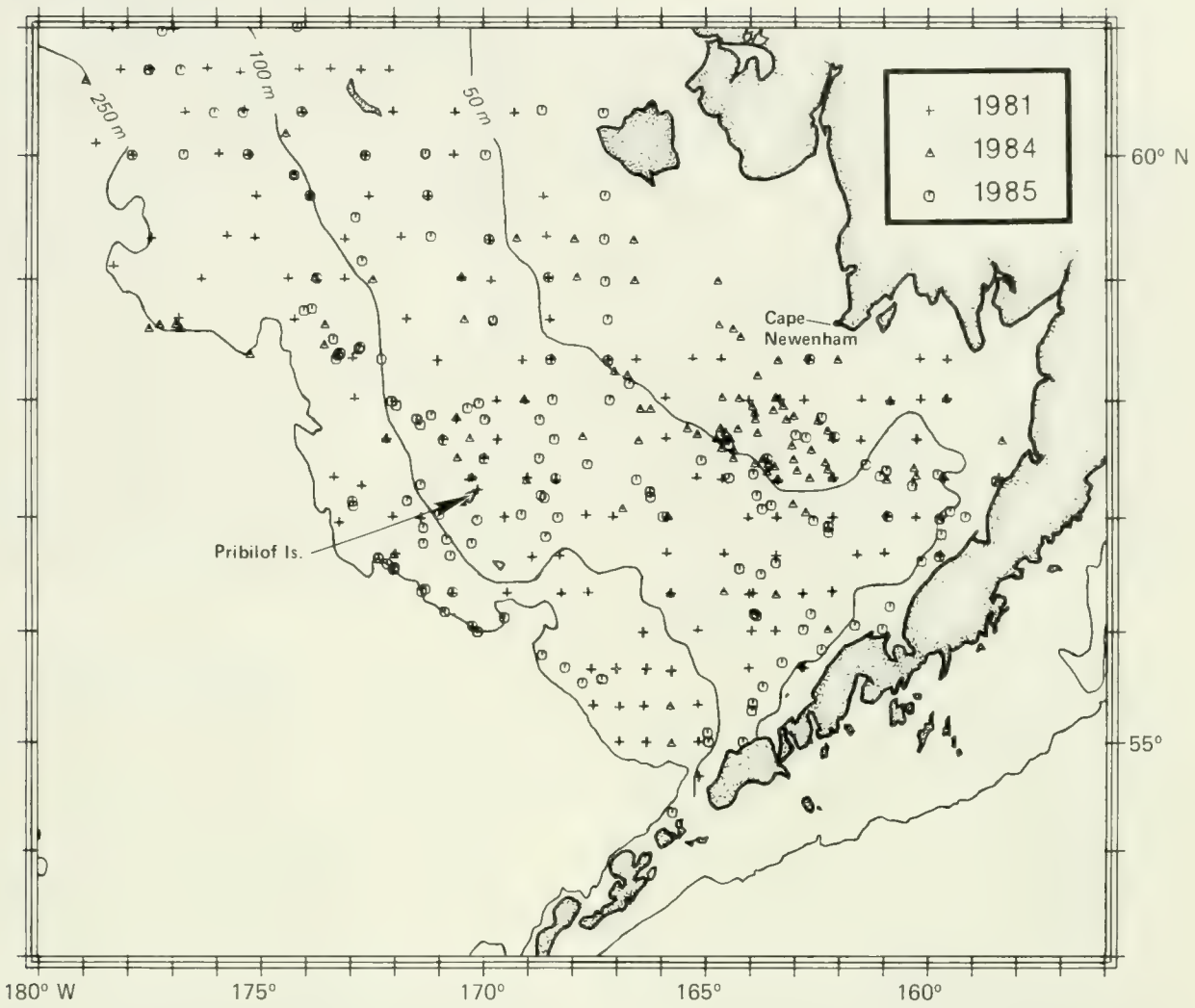

FIGURE 1.—Haul locations where Pacific cod, *Gadus macrocephalus*, stomach samples were taken during 1981, 1984, and 1985 in the eastern Bering Sea.

significance tests of the relationship between levels of each factor, so that a description of which predator sizes and sampling years had higher occurrences of crab predation could be presented.

Estimates of the total amount of each crab species consumed by the Pacific cod population during the sampling period for each year was calculated according to Mehl and Westgard (1983):

$$C_i = DR_i \cdot D \cdot B_i \cdot P_i \qquad (1)$$

where C_i is the consumption (by weight) of crab by cod belonging to size group i, DR_i is the daily ration (as a proportion of body weight daily, BWD) of cod size group i, D is the number of days in the sampling period of May through September when crab were vulnerable to predation, B_i is the biomass of cod size group i, and P_i is the proportion (by weight) of the crab species in the diet of cod size group i.

The areas of crab consumption by cod were derived by plotting the areal distribution of the percentage by weight of each species of crab in the diet for each year. A polygon encompassing the area where each species of crab was consumed was obtained for each year. The percentage by weight of a crab species in the diet of each size group of cod (P) was calculated solely from stomachs taken inside the crab consumption area. To eliminate spatial sampling bias (i.e., samples unevenly distributed within a crab consumption area), the percentage by weight of crab in the diet was calculated by taking the average of the percentages for each 20 nmi wide

square where stomachs were sampled within a crab consumption area. Since cod sometimes consume only the legs of red king crab, these stomachs were not included in the estimation of P because this behavior may not contribute to predation mortality.

Because recent studies indicate that individual prey size or weight is a more important factor influencing gastric evacuation rates in fish than prey type (Ursin et al. 1985; Jobling 1987), Pacific cod daily ration (R) was calculated using mean stomach content weight (S) in grams for each year and cod size group in the following equations from Ursin et al. (1985). These equations describe daily ration for Atlantic cod, *Gadus morhua* (whose diet and morphology are very similar to Pacific cod), as a function of mean individual prey weight (w) in grams, and bottom temperature (T) in °C:

$$R = aS \qquad (2)$$

where $a = a_0\, w^{a_1}$ and $a_0 = a_{00}\, e^{0.096T}$ and where $a_0 = 0.61\ d^{-1}$, $a_{00} = 0.33$, and $a_1 = -0.36$ for North Sea temperatures were adjusted for the Bering Sea using the average bottom temperature for Pacific cod stations sampled in each year from expendable bathythermographs obtained at most stations.

The number of days (D) when snow crab were vulnerable to predation was considered to be the whole sampling period of May through September (153 days) because predation on hard-shell juveniles of both species has been shown to occur throughout this period (Livingston et al. 1986). Although the Pacific cod's diet contains large amounts of snow crab during other times of year, geographic distribution of samples taken in other periods was not sufficient to include in the current study. Because red king crab in the hard-shell state are very spiny, cod probably consume adults only when they are in the soft-shell state. During the period sampled in this study, only female red king crab are molting (males molt earlier in the year), and their molt extends only through May of the study period ($D = 30$).

Pacific cod biomass was estimated using data collected simultaneously with stomach collections during resource assessment surveys conducted each year by the Resource Assessment and Conservation Engineering (RACE) Division of the Northwest and Alaska Fisheries Center (NWAFC). The catch per unit of effort (CPUE) of cod in kg/nmi^2 was calculated using the area swept method for each 20 nmi wide square where resource assessment trawls were performed in each crab consumption area. The cod CPUE was then separated into the CPUE for each cod size group using the length-frequency information from resource assessment surveys. Total biomass for each cod size group could then be calculated as the sum of the CPUEs multiplied by the area of 20 nmi wide square (400 nmi^2).

Population estimates and size distributions of crab from assessment surveys were provided by Robert Otto[1]. Population assessment methods for crab are described in Otto (1986).

Although size-at-age determinations are uncertain for snow crab, crab were separated into age classes using the following carapace width-at-age tables for *C. opilio* and *C. bairdi* commonly used by crab biologists at the NWAFC (J. Reeves[2]).

	Carapace width (mm)	
Age	*C. opilio*	*C. bairdi*
0	<5	<9
1	5–24	9–34
2	25–39	35–49
3	40–59	50–69
4	60–74	70–84
5	75–94	85–104
6+	≥95	≥105

Ice edge locations were taken from ice edge atlases (Joint Ice Center 1981, 1984, and 1985). These data come principally from satellite imagery. In each year, I chose the last observed southernmost ice edge extent during spring before the permanent ice retreat.

RESULTS

Geographic Distribution of Crab Consumption by Year

In all three years, red king crab were consumed by cod in the crab consumption area bounded by long. 165°00′W in the west and lat. 58°30′N at depths of 31–100 m (Fig. 2). Red king crab were found in stomachs from May through

[1]R. Otto, Kodiak Laboratory, RACE, Northwest Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Kodiak, AK 99615, pers. commun. 1986.

[2]J. Reeves, Northwest Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98115, pers. commun. May 1988.

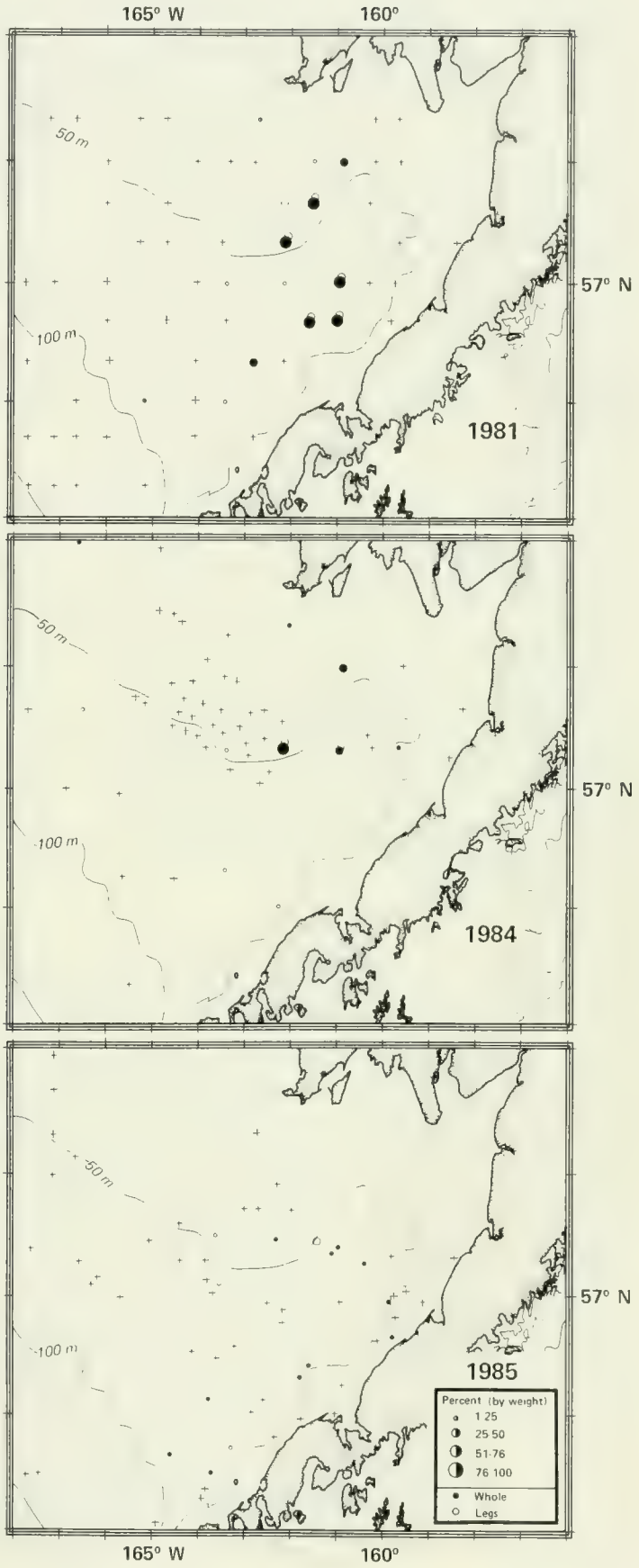

FIGURE 2.—Percentage by weight of red king crab, *Paralithodes camtschatica*, in Pacific cod stomachs by geographic location in 1981, 1984, and 1985. (Open circles denote percentage by weight of red king crab legs and black circles denote percentage by weight of whole red king crab. +'s are locations where cod were sampled but no red king crab were eaten.)

July. There was no noticeable trend over years with regard to areas where legs were consumed versus areas where whole red king crab were eaten. The percentage by weight of legs in the diet of cod at each station was generally less than 25% for all 3 years. The percentage of whole king crab eaten at each station seemed to decrease from 1981 to 1985.

The geographic distribution of *C. opilio* and *C. bairdi* in Pacific cod stomachs during 1981, 1984, and 1985 are shown in Figure 3. The figure also shows the approximate ice edge location before the final ice retreat for each year. In 1981, small percentages (<25% by weight) of *C. bairdi* were found in Pacific cod stomachs around the Pribilof Islands and also at bottom depths of 50–100 m in the area southeast of the Pribilofs. In contrast, this species was consumed over a much broader area of the southeastern Bering Sea shelf during 1984 and 1985. *Chionoecetes bairdi* also appeared in stomach contents of cod caught near the shelf edge at 200 m, even in areas northwest of the Pribilof Islands. This species was encountered in stomach contents throughout the sampling period of May through September.

In general, consumption of *C. opilio* did not overlap much geographically with the areas where *C. bairdi* were consumed, except near the Pribilof Islands. Most *C. opilio* were eaten north of the Pribilof Islands in a broad band encompassing depths from 35 to 200 m, although the highest percentages by weight in Pacific cod stomachs seemed to be in the middle shelf area with bottom depths of 50–100 m. In 1981, high percentages by weight of *C. opilio* appeared in cod diet north of 59°00′N, corresponding with the location of the ice edge before its retreat in that year. While the southward extension of predation appeared to go down to 57°30′N in 1984, the percentages by weight in the diet were not as high as in 1981. In 1985, cod diets were composed of fairly high percentages by weight of *C. opilio* as far south as 56°30′N; the ice edge in that year was at approximately the same latitude.

Differences in Diet Composition Within Areas by Year and Cod Size

Results of logistic regression of the frequencies of occurrence for each crab species in the two Pacific cod size groups for 1981, 1984, and 1985 are presented in Table 2. The most significant relationship for describing Pacific cod consumption of whole red king crab was Pacific cod size: cod larger than 60 cm contained whole red king crab more frequently than cod 30–59 cm in length. Interannual differences in frequency of occurrence of red king crab in stomachs were also significant, showing a decrease in occurrence from 1981 to 1985. Percentages by weight and frequency of occurrence of red king crab in cod stomachs followed similar year and size trends (Fig. 4).

TABLE 2.—Results from logistic regression of frequencies of occurrence of each crab species against year (1981, 1984, and 1985) and Pacific cod size group (Size 1 = 30–59 cm, Size 2 = ≥60 cm).

Crab species	Main factors chosen[1]	df	Improvement: Chi-square	Improvement: *P* value	Relationship among factor levels[2]
Paralithodes camtschatica	Size	1	29.549	0.000	Size 2 > Size 1
	Year	2	11.960	0.003	1981 > 1984 ≥ 1985
	Residual (goodness of fit)	2	(3.578)	(0.167)	
Chionoecetes bairdi	Size	1	14.832	0.000	Size 1 > Size 2
	Residual (goodness of fit)	4	(23.378)	(0.000)[3]	
C. opilio	Year	2	81.699	0.000	1985 > 1984 > 1981
	Size	1	10.341	0.001	Size 2 > Size 1
	Residual (goodness of fit)	2	(2.379)	(0.304)	

[1]Main factors chosen ($P < 0.05$) are shown in order of entry into the model.
[2]Determined from significance and sign of between-level contrasts.
[3]Chosen model has poor fit due to one anomalous cell: Size 2 in 1981 had much lower frequency of occurrence of *C. bairdi* than other cells. (Year was not significant.)

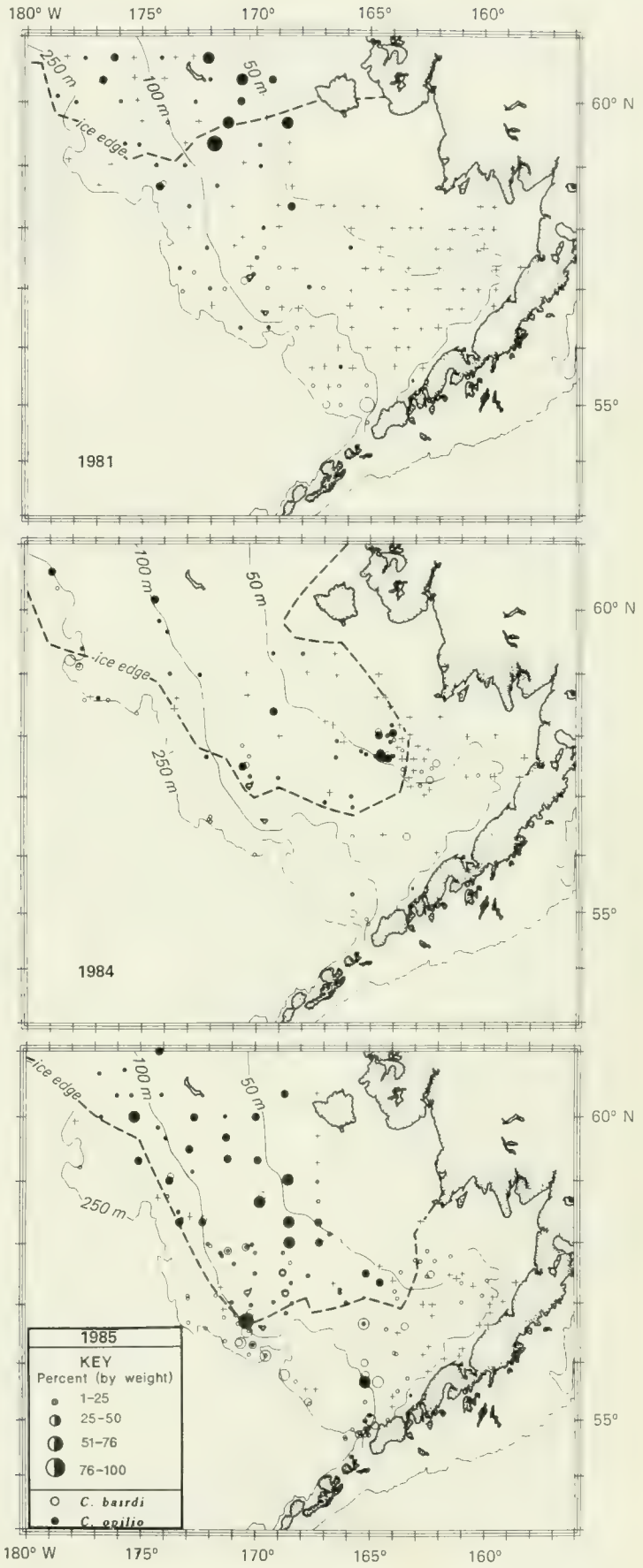

FIGURE 3.—Percentage by weight of *Chionoecetes bairdi* (open circles) and *C. opilio* (black circles) in Pacific cod stomachs by geographic location in relation to the ice edge before its last retreat in 1981, 1984, and 1985.

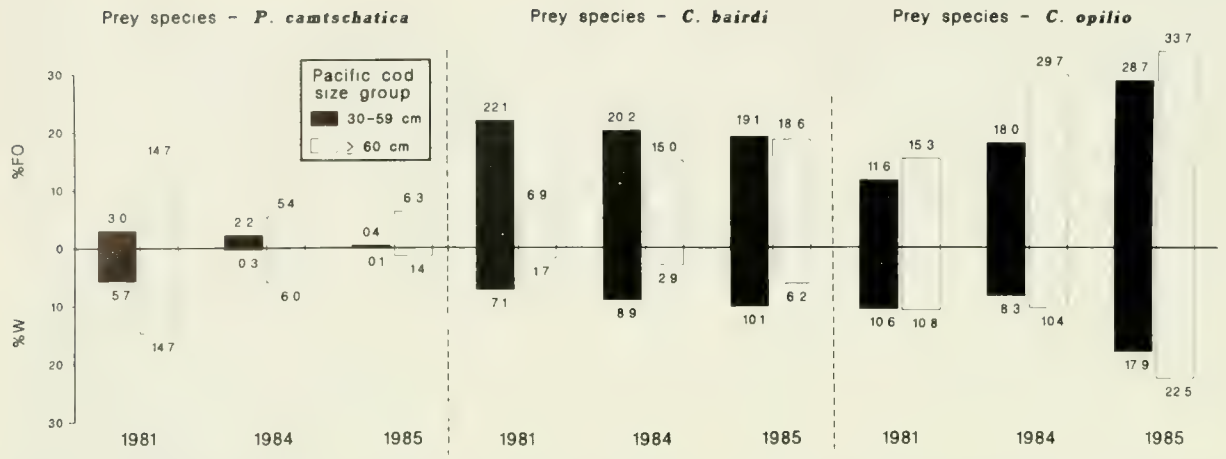

FIGURE 4.—Percentage of frequency of occurrence (%FO) and percentage by weight (%W) of red king crab, *Paralithodes camtschatica*, and two species of snow crab, *Chionoecetes bairdi* and *C. opilio*, in stomachs of two Pacific cod size groups in the respective crab consumption area during 1981, 1984, and 1985.

The only significant relationship for the occurrence of *C. bairdi* was fish size; cod 30–59 cm in length contained this crab species more frequently than cod ≥60 cm. The chosen model fits these data poorly because of the presence of one anomalous cell; cod ≥60 cm in 1981 contained *C. bairdi* much less frequently than any other group. The anomalous value produces a size-year interaction wherein small cod do not show interannual differences in the occurrence of *C. bairdi*, while large cod seem to have an increase in occurrence over time. The percentages by weight also show a size-related difference in *C. bairdi* consumption.

Year was the most important variable describing differences in occurrence of *C. opilio* in cod stomachs; occurrence increased from 1981 to 1985. Size was also significant, with large cod consuming this species more frequently than did small cod. Percentages by weight of *C. opilio* do not show the same trends as strongly as do the frequency of occurrence data; 1981 and 1984 appear similar and the size-related differences do not look as strong.

Size Frequencies and Sex Ratios of Crab Species

Only 10 red king crab CL measurements were taken over all three years because of the advanced state of digestion of most of these crabs found in Pacific cod stomachs. Carapace lengths ranged from 53 to 160 mm with an average of 106 mm. Nine out of 10 crabs were larger than 90 mm. Sex was determined for only one specimen; it was a female.

The Kolmogorov-Smirnov test (Zar 1974) showed that there was no significant difference ($P > 0.05$) between *C. bairdi* size distributions (Fig. 5) consumed by cod 30–59 cm in 1984 and 1985, and no significant size difference between *C. bairdi* consumed by cod ≥60 cm in 1981, 1984, and 1985. All other size-frequency distribution comparisons, in particular comparisons between cod size groups within years, showed significant differences. Most *C. bairdi* in smaller cod (30–59 cm) were <20 mm CW, while large cod consumed crab in the 20–30 mm CW size range. Size distributions of crab <95 mm CW from survey results show size-frequency modes at 40 mm CW or greater. In 1981, most crab in the survey were >60 mm CW.

The only size-frequency distributions of *C. opilio* (Fig. 6) that were not significantly different ($P > 0.05$) from each other were those for smaller cod (30–59 cm) in 1984 and 1985. The size distributions of *C. opilio* consumed during 1981 by both cod size groups were very different from size distributions for the other 2 years. Smaller cod during that year ate more crabs larger than 30 mm CW than in other years, and the modal crab size consumed by large cod (≥60) was also greater (40–50 mm CW) compared to 1984 and 1985. Crab size distributions from the survey show size frequency modes at 40–50 mm CW.

The proportions of female snow crabs in Pacific cod stomachs and in resource assessment trawl surveys were determined (Table 3). In cod stom-

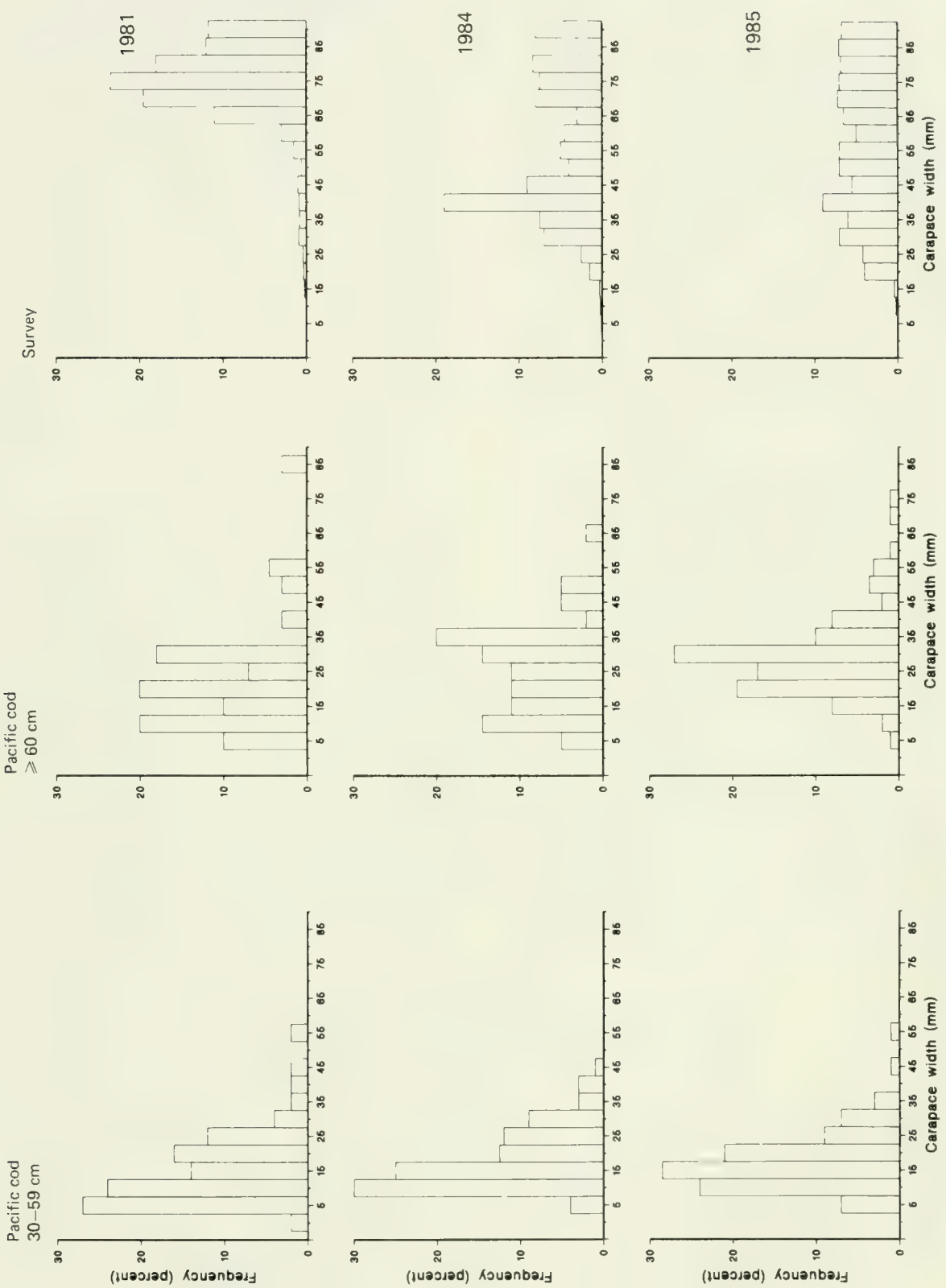

FIGURE 5.—Relative size-frequency distribution of *Chionoecetes bairdi* in stomachs of two Pacific cod size groups and in the resource assessment survey during 1981, 1984, and 1985.

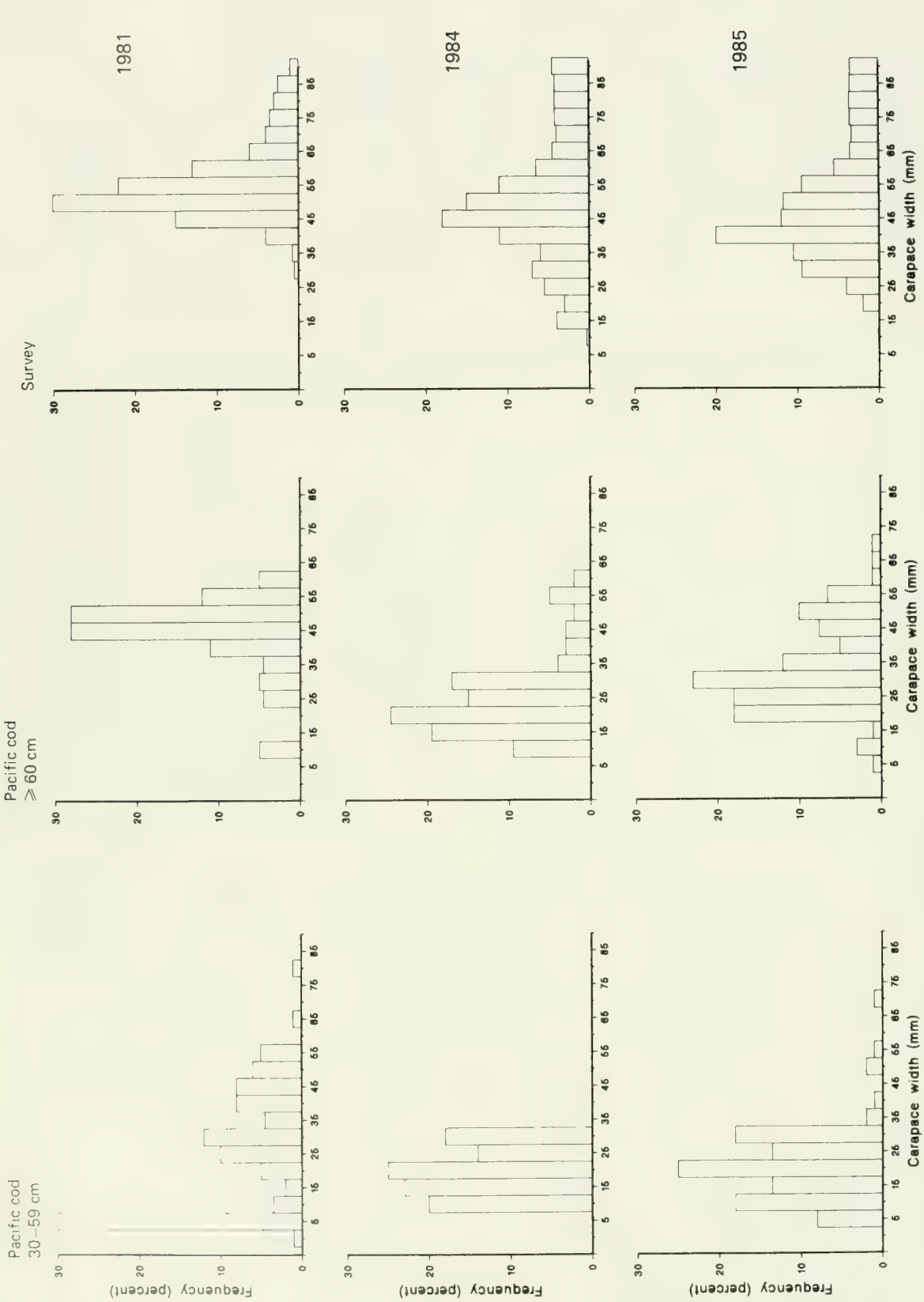

FIGURE 6.—Relative size-frequency distribution of *Chionoecetes opilio* in stomachs of two Pacific cod size groups and in the resource assessment survey during 1981, 1984, and 1985.

TABLE 3.—Total number (*N*) and proportion of female snow crabs (PF), *Chionoecetes bairdi* and *C. opilio*, in Pacific cod stomachs and resource assessment trawl surveys for the years 1981, 1984, and 1985 in the eastern Bering Sea.

		Stomachs		Survey[1]	
Crab species	Year	*N*	PF	*N*	PF
C. bairdi	1981	248	[2]0.935	6,774	0.675
	1984	180	[3]0.567	5,770	0.645
	1985	817	0.557	2,664	0.567
C. opilio	1981	77	[2]0.857	22,728	0.640
	1984	165	[3]0.557	19,709	0.510
	1985	512	0.607	12,125	0.426

[1]Sex ratios and number of crab sexed provided by Resource Assessment and Conservation Engineering Division, Kodiak Laboratory for crab <95 mm CW.
[2]Crab sex was not consistently recorded by stomach analysts during this year.
[3]Observed proportion was not significantly different from 0.5 ($P > 0.05$) using the normal approximation to the binomial test.

achs, the proportions of females for both species of snow crabs during 1981 were much larger than other years. In 1984 and 1985, the proportions of females in cod stomachs were fairly close to 0.5, although in the normal approximation to the binomial test (Zar 1974) only the proportions in 1984 were not significantly different ($P > 0.05$) from 0.5; a test of an even sex ratio. Trawl survey estimates of the proportion of female snow crab <95 mm CW range from 0.43 to 0.67. In some cases the proportion of females observed in stomach contents differed from the proportion estimated from the trawl survey. No trends seem readily apparent except that trawl survey estimated proportions, and those proportions in Pacific cod stomach contents were more similar in 1984 and 1985 than during 1981.

Pacific Cod Population Consumption of Crab

Daily ration estimates range from about 0.5 to 0.9% BWD with small cod consuming larger rations as a percentage of their body weight than large cod in a given year (Table 4). Rations for both cod groups were smaller in 1985 than in 1981 and 1984 because of the lower bottom temperature and the large individual prey weight for large cod in that year.

The parameters necessary for calculating population consumption are the cod biomass in the prey area, the percentages by weight of each crab species in the diet, and the number of days the crab species is vulnerable to cod predation (Tables 5–7). The calculations for the total amount of red king crab consumed by cod assume that only female crabs are consumed, and the period of predation vulnerability during the sampling period is 30 days in May when female crabs are in the soft-shell condition. Further, because of the small number of crabs measured from stomach contents in each year, the average carapace length of all red king crab measured in a year was used to calculate the total number of crab consumed (1981 = 104 mm CL and 1984–85 = 111 mm CL; corresponding to about age 6 for females).

Both total biomass and numbers of red king crab consumed by cod declined from 1981 to 1985 by a factor of 10 (Table 5). The total amount of *C. bairdi* consumed by cod during the 153 d sampling period in each year, in terms of total weight and numbers, decreased slightly from 1981 to 1984 and increased about threefold from 1984 to 1985 (Table 6). Although the total biomass of *C. opilio* consumed by cod dropped dur-

TABLE 4.—Parameters used to derive daily ration estimates and the estimated daily rations for two size groups of Pacific cod in 1981, 1984, and 1985 in the eastern Bering Sea. (% BWD is percentage of body weight daily.)

		Average weight (g)			Bottom temperature	Daily ration
Year	Cod size group	Cod	Individual prey	Cod stomachs	(°C)	(% BWD)
1981	30–59	1,340	1.02	25.1	3.7	0.86
	≥60	4,045	12.31	141.4	3.7	0.66
1984	30–59	1,095	0.48	16.7	3.1	0.87
	≥60	4,994	6.55	180.7	3.1	0.80
1985	30–59	1,217	1.00	18.7	2.3	0.63
	≥60	5,383	18.67	180.0	2.3	0.47

TABLE 5.—Parameters used to obtain cod population consumption estimates for *Paralithodes camtschatica* and the estimated total biomass and numbers consumed by the cod population. (Assuming this species of crab is vulnerable to cod predation for only 30 days of the study period.)

Year	Cod size (cm)	Cod biomass (1,000 t)	Percent crab in diet (by weight)	Total biomass crab consumed (1,000 t)	Total number crab consumed (millions)
1981	30–59	118	5.7	1.7	2.00
	≥60	39	14.7	1.1	2.00
			Total	2.8	4.00
1984	30–59	72	0.3	0.1	0.06
	≥60	127	6.0	1.8	2.00
			Total	1.9	2.06
1985	30–59	89	0	—	—
	≥60	103	1.4	0.2	0.20
			Total	0.2	0.20

TABLE 6.—Parameters used to obtain cod population consumption estimates for *Chionoecetes bairdi* and the estimated total biomass and numbers consumed by the cod population. (Assuming this species of crab is vulnerable to cod predation during the whole 153 days of the study period.)

Year	Cod size (cm)	Cod biomass (1,000 t)	Daily ration (%BWD)	Percent crab in diet (by weight)	Total biomass crab consumed (1,000 t)	Total number crab consumed (billions)
1981	30–59	122	0.86	7.1	11.4	2.71
	≥60	140	0.66	1.7	2.4	0.10
				Total	13.8	2.81
1984	30–59	51	0.87	8.9	6.0	0.91
	≥60	164	0.80	2.9	5.8	0.31
				Total	11.8	1.22
1985	30–59	224	0.63	10.1	21.8	3.87
	≥60	246	0.47	6.2	11.0	0.51
				Total	32.8	4.38

TABLE 7.—Parameters used to obtain cod population consumption estimates for *Chionoecetes opilio* and the estimated total biomass and numbers consumed by the cod population. (Assuming this species of crab is vulnerable to cod predation during the whole 153 days of the study period.)

Year	Cod size (cm)	Cod biomass (1,000 t)	Daily ration (%BWD)	Percent crab in diet (by weight)	Total biomass crab consumed (1,000 t)	Total number crab consumed (billions)
1981	30–59	274	0.86	10.6	38.2	1.72
	≥60	136	0.66	10.8	14.8	0.28
				Total	53.0	2.00
1984	30–59	100	0.87	8.3	11.0	2.00
	≥60	164	0.80	10.4	20.9	1.29
				Total	31.9	3.29
1985	30–59	185	0.63	17.9	31.9	4.06
	≥60	173	0.47	22.5	28.0	1.03
				Total	59.9	5.09

ing 1984 compared with 1981 and 1985, the total number of crab consumed increased over the whole time period, reflecting the smaller sizes of crab consumed in 1984 and 1985 (Table 7).

Total numbers by age of *C. bairdi* and *C. opilio* consumed are shown in Figures 7 and 8. Most *C. bairdi* consumed are age 1, but ages 0, 2, and 3 are also represented. This figure does not show the small amount (3 million) of age 5 crab eaten in 1981 or the 5 million age 4 crab eaten during 1985. Cod consumption of *C. opilio* is mainly directed at crab of ages 1–2. More *C. opilio* of ages 3–4 are eaten than *C. bairdi*.

DISCUSSION

The geographic distribution of Pacific cod predation on red king crab corresponds to the main area of red king crab abundance from NMFS resource assessment trawl surveys. These surveys produce relatively precise abundance estimates for crab >75 mm CL (Otto 1986) which is

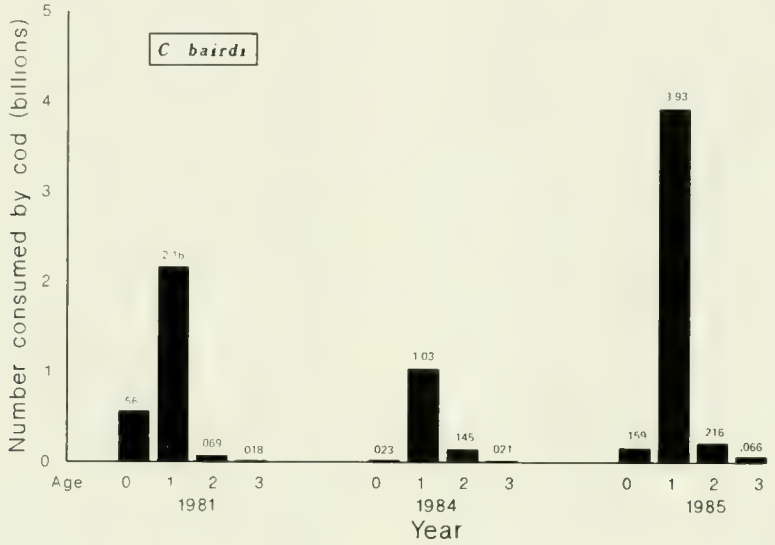

FIGURE 7.—Total number by age group of *Chionoecetes bairdi* consumed by the Pacific cod population in 1981, 1984, and 1985.

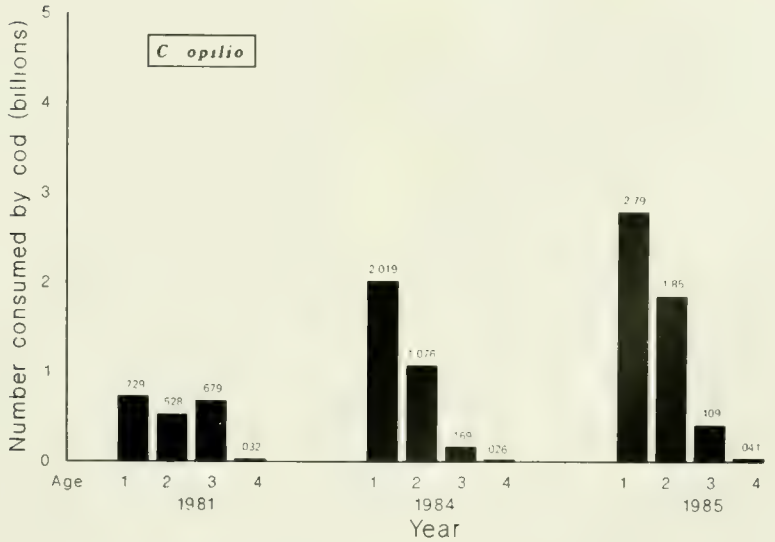

FIGURE 8.—Total number by age group of *Chionoecetes opilio* consumed by the Pacific cod population in 1981, 1984, and 1985.

the size range of red king crab consumed by cod in this study. However, the areas of cod predation on snow crab show interannual variation that does not match areas of adult abundance determined from NMFS trawl surveys, probably because the trawls used in these surveys do not catch small snow crabs <40 mm CW, which is the size consumed most by cod. Surveys showed most adult *C. bairdi* to be east and southeast of the Pribilof Islands in 1981, 1984, and 1985, while cod stomach contents showed no small *C. bairdi* east of 165°00′W in 1981. Similarly, surveys showed high densities of *C. opilio* >95 mm CW as far south as the Pribilofs in 1981, whereas most small *C. opilio* eaten by cod were much farther north in that year.

The geographic distribution of snow crab predation by Pacific cod was very different in 1981 than in the other two years, and the more northerly location of the ice edge in that year relative to 1984 and 1985 suggests an environmental relationship between *C. opilio* distribution and physical factors. Somerton (1981, 1982) postulated a direct relationship between spring ice cover and planktonic larval survival of *C. opilio* in order to explain observed high recruitment to the adult population of those year classes that may have been in the plankton and benefited from the associated ice edge production during 1971 and 1972 in the eastern Bering Sea. Instead of a relationship between ice cover and planktonic survival, however, our data suggest that ice cover in a given year may also indicate the areal extent of juvenile *C. opilio* in the same year. Since benthic dwelling juveniles would not benefit directly from an ice edge bloom, the ice edge in a particular year may be an indicator of another environmental variable such as bottom temperature.

The average bottom temperature at stations where *C. opilio* were found in cod stomachs is compared (*t*-test) with bottom temperatures where no *C. opilio* were consumed during the three years of this study (Fig. 9). The average bottom temperatures (≤3°C) were significantly lower ($P < 0.05$) for the locations where *C. opilio* were found than for locations where they were absent. Somerton (1981) reported the weighted average bottom temperatures at stations where *C. opilio* occurred in 1979 was less than 3°C when the weights used were crab abundance. In that year, juveniles <40 mm CW had the highest abundances per station, indicating that the temperatures apply mainly to the juvenile portion of the population. In the northwest Atlantic, Brêthes et al. (1987) found bottom temperatures <3°C to be the most significant factor in determining the spatial distribution of juvenile *C. opilio* <40 mm CW in the Gulf of St. Lawrence. Thus, the geographic distribution of juvenile *C. opilio* appears to depend mostly on bottom temperature; highest densities are found in areas where bottom temperatures are less than 3°C and those areas may be a significant portion

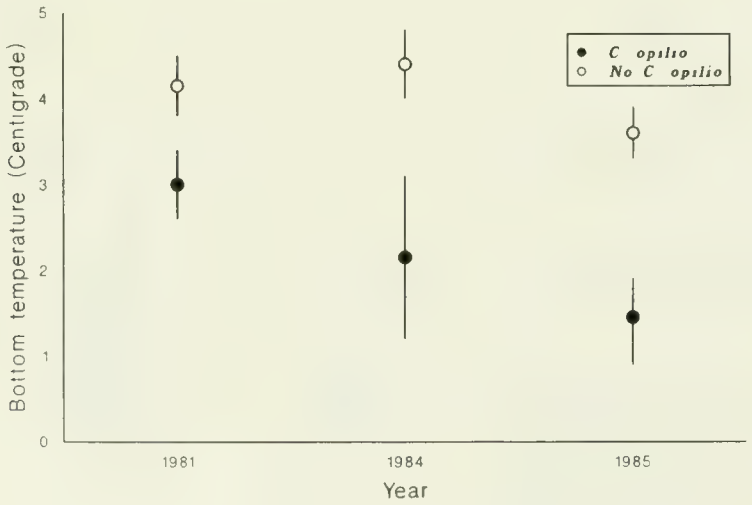

FIGURE 9.—Mean bottom temperature (°C) and 95% confidence intervals at locations where Pacific cod consumed *Chionoecetes opilio* (black circles) and at locations where Pacific cod did not contain *C. opilio* (open circles) in 1981, 1984, and 1985.

of the eastern Bering Sea shelf in cooler years.

Diet Composition by Year and Cod Size

Analysis of frequencies of occurrence of red king crab in Pacific cod stomachs through logistic regression shows that cod size is the most important factor in determining consumption of whole red king crab; the frequency of occurrence was significantly greater in cod larger than 60 cm FL. Blau (1986) found that Pacific cod, which presumably had consumed soft-shell female king crabs in the Kodiak region of the Gulf of Alaska, ranged in size from 45 to 79 cm FL. That study, however, did not examine differences in frequency of occurrence within that size range, and none of the crab eaten were whole. Interannual differences in red king crab consumption were significant in our study, decreasing from 1981 to 1985. NWAFC abundance estimates for the female portion of the red king crab population show a corresponding trend with a decrease in numbers from 103.6 million in 1981 to 13.7 million in 1985. This suggests that individual cod predators responded to decreases in crab density by consuming less crab.

Although logistic regression of *C. bairdi* frequencies of occurrence showed cod size as an important variable, the model fit was poor due to the low frequency of crab occurrence in cod ≥60 cm FL in 1981. If the percentages by weight are examined (Fig. 4), the size relationship looks clearer. Smaller cod consistently ate more than large cod, and the interannual changes within size groups showed consistent, small increases across years. NMFS surveys are not able to provide precise estimates of crab <40 mm CW, not only because of escapement through trawl meshes, but also because snow crab <100 mm CW have a greater tendency to bury themselves in bottom sediments (Conan and Maynard 1987), reducing their vulnerability to trawl capture. If cod respond to changes in *C. bairdi* density as they appear to do for red king crab density, then our data suggest the possibility of stable or slight increases in juvenile *C. bairdi* population numbers for crab <40 mm CW over the three study years. The similarity of *C. bairdi* size distributions in cod stomachs for the three years within each cod size group further supports the suggestion of stable juvenile (<40 mm CW) *C. bairdi* population size distributions over time.

The model which best explains *C. opilio* consumption by cod shows year as the most important variable (with consumption increasing over years) and size as the next important variable (with larger cod consuming *C. opilio* more frequently than smaller cod). If the occurrence of juvenile crab <40 mm CW in cod diets can be used as a measure of juvenile crab abundance in the survey area, then our data show a probable increase in juvenile *C. opilio* abundance from 1981 to 1985. Waiwood and Elner (1982) similarly suggested that the increase in Atlantic cod, *Gadus morhua*, predation on snow crab observed in 1980 and 1981 in the Gulf of St. Lawrence in the northwest Atlantic was due to increased availability of small crabs. The size-frequency distributions of *C. opilio* in cod stomachs also indicate more *C. opilio* <35 mm CW in 1984 and 1985 than in 1981 at least in the survey area. Somerton (1981) showed that large numbers of *C. opilio* juveniles exist north of 61°00′N, an area which was not sampled in this study. It is possible that in colder years such as 1984 and 1985, an influx of juvenile *C. opilio* from these northern areas could have entered southeastern Bering Sea shelf waters and have become more available to cod. Of course, there is a limit to the distance juvenile crab can migrate in one year. The observed downward shift in mean size and increased numbers of *C. opilio* in cod stomachs may not be the result of actual increases in juvenile *C. opilio* abundance but might be the result of progressive southerly shifts in the geographic distribution of small juveniles in progressively colder years. More years of data need to be examined, however, to determine what happens to juvenile distributions over time, particularly between two consecutive years with very different climatic conditions.

Because of the large carapace lengths of red king crab consumed by cod (50–160 mm CL), the well-digested nature of red king crab in stomachs, the usual occurrence of whole crab only around May, and the fact that one red king crab's sex was determined to be female, we have assumed that Pacific cod consume soft-shell females, which molt in Bristol Bay around April to May (Hayes 1983). It seems highly unlikely that cod could consume whole crab of those carapace lengths in a hard-shell condition. Blau (1986) also found cod consuming red king crab during the king crab molting period in the Gulf of Alaska. Because male red king crab molt in winter while migrating to the mating grounds (Powell and Nickerson 1965), our assumption that only soft-shell females are consumed in spring seems supportable. This does not rule out the possibility that cod may consume soft-shell males, which

molt during winter. However, our winter sampling coverage has been limited and has not detected this type of occurrence.

With the exception of 1981, when stomach analysts did not consistently record snow crab sex, the proportions of female juvenile snow crabs in stomach contents were close to 0.5 and were not significantly different from a 1:1 ratio of females to males in 1984. Adams (1979) reviewed the literature on *C. opilio* and found that the early life history of males and females are similar with respect to size, growth, distribution, and habitat. Brêthes et al. (1987) found sex ratios of *C. opilio* <30 mm CW in the northwest Atlantic to be 1:1 with no spatial segregation of sexes. The proportions of female snow crabs <95 mm CW in the NMFS assessment surveys were close to 0.5 in most years. Thus, cod do not appear to be selecting snow crab on the basis of sex and are probably preying randomly on individuals on the basis of crab size.

Pacific Cod Population Consumption of Crab

Daily rations that were derived using the Ursin et al. (1985) model for incorporating prey size effects on gastric evacuation rate appear reasonable compared with estimates of daily ration for Atlantic cod from areas with bottom temperatures higher than temperatures in the eastern Bering Sea. My estimates ranged from 0.47 to 0.86% BWD; and estimates for Atlantic cod of similar sizes range from 0.5 to 1.0% BWD in the North Sea (Daan 1973), 1.6 to 2.0% BWD in the Faroe plateau (Jones 1978), and 0.5 to 1.9% BWD on Georges Bank (Durbin et al. 1983). Livingston et al. (1986) calculated daily ration for Pacific cod using the Elliott and Persson (1978) model without correction for prey size effects using a subset of the data presented in this paper and obtained values of 0.31% BWD for cod <55 cm FL and 1.30% BWD for cod >55 cm FL. When compared with cod growth data, however, the rations for small cod were too small to account for growth, and rations for large cod were too large. The current approach seems to correct for the deficiencies in the previous estimates, and produces ration values which are not so divergent for the two cod size groups.

Other parameters involved in estimating population consumption are also subject to error: predator biomass estimates, the percentage of prey items in the predator's diet, and the number of days the crab species is vulnerable to predation. NMFS survey estimates of cod biomass in recent years have 95% confidence intervals of 12–18% of the mean biomass estimate (Thompson and Shimada 1987), a minimum confidence interval because of the assumptions of complete vulnerability and catchability of cod to bottom trawls. Cod also performed seasonal onshore-offshore migrations (Wespestad and Shimada 1984); a factor not taken into consideration here that could change the biomass of cod in a particular area over the time period in this study. Errors in diet composition parameters can arise from insufficient sample sizes, uneven spatial distribution of samples, and possible diet changes over space and time scales not considered in this study. Sampling effort for cod stomachs was widely distributed over the whole shelf area during 1981 and 1985, but some areas were not sampled well during 1984 (Fig. 1). I have attempted to reduce bias in diet composition estimates that may arise from uneven stomach sample sizes within areas by averaging diet percentages estimated for each 20 nmi wide square where stomachs were sampled within a crab consumption area. A similar practice has been adopted in the North Sea stomach sampling program, which provides diet composition estimates for a multispecies virtual population analysis model (Mehl 1986). In this study, I have estimated consumption that occurred only during May through September, so the estimated numbers of snow crab consumed by cod apply only to that portion of the year. Livingston et al. (1986) has shown that Pacific cod in the eastern Bering Sea consume snow crab throughout the whole year; therefore, the estimates presented in this paper can be considered mainly as indexes of the total numbers consumed by cod. There is also great uncertainty about the size at age for crabs and the allocation of crab size groups to age classes should be considered approximate.

Impact on Crab Populations

Predation mortality rate of a prey population must increase with prey population size in order to demonstrate that a predator population is regulating the size of the prey population (Holling 1959). NMFS resource assessment surveys provide annual estimates of female red king crab abundance, which can be compared with the total cod population removals of female red king crab in the same year (Fig. 10). Both the female red king crab population and the estimated removals from the population by cod follow the

FIGURE 10.—Total number of red king crab, *Paralithodes camtschatica*, eaten by the Pacific cod population during 1981, 1984, and 1985 compared with resource assessment estimates of the total female red king crab population during the same years. (Note different y-axis scales.)

same pattern of linear decline. Removals, expressed as a percentage of the population, are 3.8%, 2.8%, and 1.4% for the years 1981, 1984, and 1985, respectively. The declining percentages removed actually indicate weak compensatory density-dependent mortality over time, which appears to be mainly due to the functional response of individual cod to declining prey populations (i.e., a decline in the average amount of crab per predator with a decline in crab population). Thus, at least over the range of female red king crab population sizes considered here, it appears that cod predation is not responsible for the observed declines in female red king crab populations from 1981 to 1985. The percentages removed by cod form a small and declining part of the total population decline. Since the period of red king crab vulnerability to cod predation for the present study included only 30 out of a possible 60 days when red king crab females are in the soft-shell condition, the estimated removals could be doubled to approximate total annual amounts removed by cod. This would affect the percentage of removals in each year by a factor of two but would not change the seemingly compensatory density-dependent relationship between crab removals and crab population size.

A similar comparison cannot be made directly for cod consumption of the two snow crab species because cod consume mostly age 1 crab, which are not well estimated in NMFS research surveys. However, the numbers of age 1 snow crab eaten in a particular year can be compared to the number of age 3 crab collected 2 years later in NMFS research surveys, which should be more precise (Figs. 11, 12). Although the curves of age 1 crab consumed and the number of age 3 crab found 2 years later in the trawl surveys appear to be somewhat similar in shape for *C. bairdi* for the 3 years, the estimated numbers of age 1 crab consumed in a particular year are about two orders of magnitude greater than the numbers of age 3 crab found 2 years later. This at least indicates that cod are responsible for removing large numbers of age 1 crab relative to the number that remain at age 3. The unequal ratios of prey removed to prey remaining among years could also indicate that density-dependent removals are occurring.

The numbers of age 1 crab in the population can be reconstructed, as in Forney (1977), by adding the number remaining at age 3 to the number of age 1 eaten by cod. This assumes that cod predation is the major source of mortality for crab less than age 3 and that virtually all of this mortality occurs at age 1. If removals by cod are calculated as a percentage of the reconstructed population size, then the values obtained for 1981, 1984, and 1985 are 84%, 95%, and 94%, respectively. These percentages are substantial

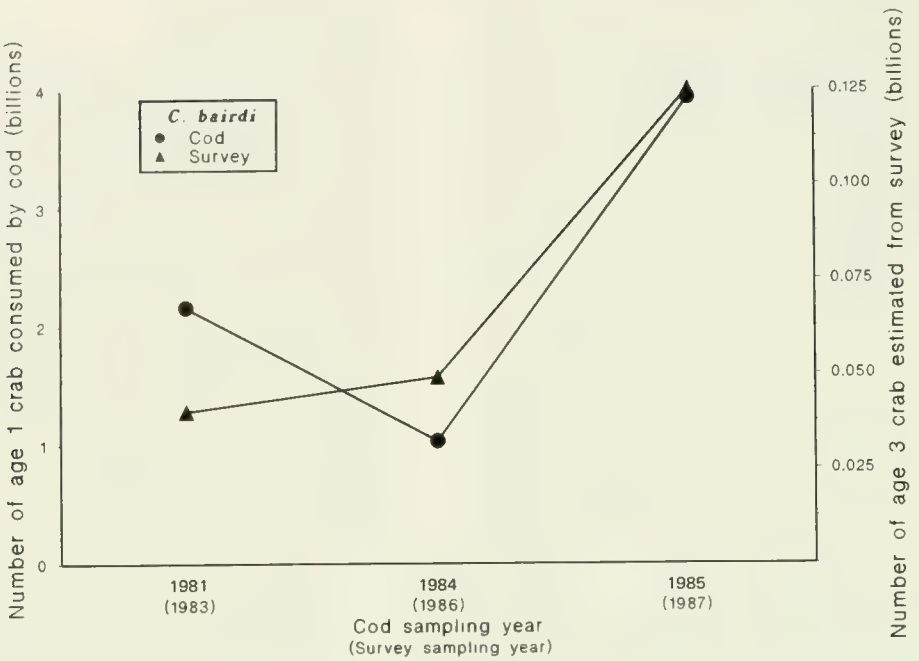

FIGURE 11.—Total number of age 1 *Chionoecetes bairdi* snow crab eaten by the Pacific cod population during 1981, 1984, and 1985 compared with resource assessment estimates of the age 3 population in 1983, 1986, and 1987. (Note different y-axis scales.)

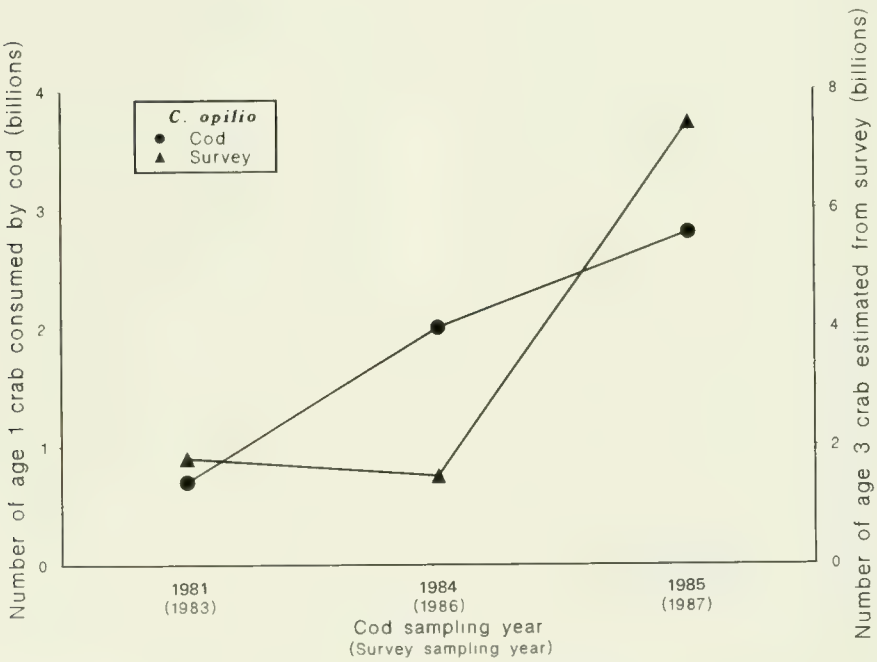

FIGURE 12.—Total number of age 1 *Chionoecetes opilio* snow crab eaten by the Pacific cod population during 1981, 1984, and 1985 compared with NWAFC resource assessment estimates of the age 3 population in 1983, 1986, and 1987. (Note different y-axis scales.)

portions of the estimated age 1 population and could be an indication of overestimation of the population consumption by cod, underestimation of the age 1 population size because of unaccounted sources of mortality or underestimation of age 3 numbers by research trawl surveys. As mentioned earlier, cod have been shown to consume snow crab throughout the year in the eastern Bering Sea so the current estimate of 153 days for vulnerability to predation by cod is an underestimate. Further, the cod diet contained fair amounts of snow crab that could not be identified to the species level due to state of digestion and were not included in the estimates. This again leads to conservative estimates of the total number of snow crab consumed by cod.

A similar comparison of *C. opilio* removals at age 1 by cod with trawl survey estimates of numbers remaining at age 3 shows that numbers remaining at age 3 are greater than those eaten at age 1 during 1981 and 1985. Percentages removed of the reconstructed age 1 cohort would be 28%, 57%, and 27% for 1981, 1984, and 1985, respectively. These percentages are overestimates because substantial numbers of age 2 *C. opilio* are also eaten (Fig. 8) but not included in the reconstructed population estimate.

Although these estimates are subject to many sources of error, the high predation mortality rates of juvenile crab found here may not be unrealistic. Using food habits data to quantify predation removals, multispecies virtual population analysis of North Sea fish stocks produced average annual instantaneous predation mortality coefficients ranging from 0.2 to 1.8 for age 1 fish in the model (Daan 1987). Large interannual differences in predation mortality coefficients were observed within fish species, suggesting that predator populations were exerting density-dependent control on some year classes. Similarly, our study has shown the possibility of large predation removals of mostly age 1 snow crabs and some interannual variation in the percentages removed. The impact on *C. bairdi* seems greater than on *C. opilio*, at least for age 1 crab. *Chionoecetes bairdi* are also more vulnerable to cod predation because of their high spatial overlap with cod populations. In contrast, unknown portions of the *C. opilio* juvenile population are north of the main survey area, and the main center of their distribution may shift south into areas populated by cod in some years.

Analysis of a longer time series of cod predation data may help locate abundant crab year classes and allow us to track their numbers over time. There is uncertainty about the growth patterns of juvenile snow crabs, and following size class modes in cod stomach data in succeeding years may provide more clues to these growth patterns. Further, although this study does not attempt to explain factors influencing early life history survival, it does suggest that predation is an important factor influencing survival of ages 1 and 2 snow crab.

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A Comparative Analysis of Growth Zones in Four Calcified Structures of Pacific Blue Marlin, *Makaira nigricans*

Kevin T. Hill, Gregor M. Cailliet, and Richard L. Radtke

ABSTRACT: Sagittae, vertebrae, and anal and dorsal fin spines collected from Pacific blue marlin in Kona, Hawaii were evaluated for legibility and interpretability of growth patterns, ease of collection and processing, and the precision of the resultant annulus counts for use in estimating age. Sagittae, and anal and dorsal fin spine sections contained growth zones assumed to be annual events and there was a linear relationship between age estimates of corresponding samples. Vertebrae had numerous minute growth increments, but contained no marks which could be interpreted as annual. While nonparametric tests revealed no significant difference between age estimates from different hardparts of the same fish, dorsal and anal spine counts had the best agreement. Anal and dorsal fin spines were more practical in terms of ease of collection, processing, legibility, and interpretation; however, age estimates of spine samples from larger fish required a statistical replacement of inner growth zones that were destroyed by matrix expansion. Although more difficult to collect and interpret, sagittae provide more detailed age information. Mean length-at-estimated age data based on anal spine band counts are also presented.

Increased knowledge of billfish age and growth is essential for sensible management of these fisheries. Although there is a paucity of such information for most billfish species, the Western Pacific Fisheries Management Council was forced to draft a management plan for the Pacific blue marlin, *Makaira nigricans*, with only cursory data (WPFMC 1985). This lack of information is due to the many difficulties involved with studies of large pelagic fish species (Prince and Pulos 1983), compounded by lack of routine sampling programs by research agencies in the Pacific region.

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Various calcified structures have been utilized for age estimation of the Istiophoridae. Dorsal spine sections have provided age estimate data for Atlantic sailfish, *Istiophorus platypterus* (Jolley 1974, 1977; Hedgepeth and Jolley 1983), Atlantic white marlin, *Tetrapterus albidus*, and Atlantic blue marlin, *Makaira nigricans* (Prince et al. 1984). Sagittal otoliths have been described as potentially useful structures for ageing most billfish species (Radtke 1981, 1983; Radtke and Dean 1981; Radtke et al. 1982; Prince et al. 1984; Wilson 1984; Cyr 1987). Jolley (1974) described numerous circuli in the vertebrae of sailfish; however, both scales and vertebrae have now been dismissed as structures for age estimation in billfish (Prince et al. 1984).

Age estimation of Pacific blue marlin is still in the developmental stages, and most data have focused on sagittae (Radtke 1981; Wilson 1984), with little effort on other skeletal structures. The objective of the present study was to examine, interpret, and quantitatively compare growth patterns in the sagitta, vertebrae, and dorsal and anal fin spines of blue marlin from Kona, HI. Each structure was evaluated in terms of ease of collection and processing, legibility of growth patterns, and the relative precision of the resulting age estimates.

MATERIALS AND METHODS

Pacific blue marlin were sampled at the Hawaiian International Billfishing Tournaments in Augusts 1982 (n = 48), 1983 (n = 113), and 1984 (n = 98), and at the Kona Gold Jackpot tournament in May 1983 (n = 20), Kailua-Kona, HI. Additional spine samples were obtained from the Pacific Gamefish Research Foundation (n = 32), the Hawaii Fishing Agency (n = 2), and the National Marine Fisheries Service, Southeast Fisheries Center (a specimen from Kona which was shipped to Miami for taxidermy). Meristic data collected for each fish included lower jaw-fork length (LJFL to 0.1 cm),

roundweight (W to 0.5 lb converted to kg), sex, and date of capture (Hill 1986).

Anal and Dorsal Fin Spine Analyses

Anal and dorsal fin spines were collected and prepared for analysis following modified methods of Prince et al. (1984) (Hill 1986). The second anal spine and sixth dorsal spine were selected for age analysis. These were chosen because they were the thickest of the spine complex, and sections taken from spines anterior to these had more prominent core matrices.

Spine length, defined as the distance from the hole at the center of the condyle base to the spine tip, was measured to the nearest millimeter. Thin cross sections from anal and dorsal fin spines were taken at positions marked at 10% and 5% (respectively) of the spine length from the condyle hole. Spine sections were examined using a compound stereoscope at 63× and 120× magnification using either transmitted light or reflected light with a black background. The focus of the spine was defined as the midpoint of the distance between the anterior and posterior portions of the spine along the midsagittal plane. All growth bands were counted and their radii measured with an ocular micrometer along the plane from the focus of the spine to the widest radius of the spine section. Spine radius (anal spine radius = AR; dorsal spine radius = DR) was defined as the distance from the focus to the outside edge of the spine along the same plane.

Statistical replacement of early missing anal and dorsal spine growth bands in larger fish was accomplished by summarizing band radii statistics from smaller, younger specimens in which these early bands were visible. Compiled band radius statistics included spine samples which had at least the first or second band visible. Unpaired t-tests were applied to compare corresponding radii between those specimens containing the first and second band and to compare corresponding band radii between sexes.

Final corrected age estimates were assigned to spine samples missing early bands by comparing the radii of the first four visible bands to the means and 95% confidence limits of the compiled data. When the radii of at least three successive bands of the first four visible bands fitted well within the 95% confidence limits of three or four bands of the compiled data, corresponding ages were assigned. The use of this technique to provide final age estimates was based upon the assumption that there was a predictable number of growth bands per millimeter of radius in the core matrix, and that the first several visible bands were analogous in age to matching bands of the compiled radius data.

Sagitta Analyses

Sagitta were cleaned, prepared, and examined following the methods of Radtke (1983) and Hill (1986). Terminology for sagitta orientations is based on Prince et al. (1986). Sagittal otolith weight (SW) was measured to the nearest 0.005 mg. Age assignments were based on combined counts of external growth features present on the sagittae, which included ridges along the anterior rostrum edge on the ventral plane of growth and ridges along the ventral surface of the medioventral and medial planes of growth.

Previous studies of Istiophorid sagitta have supplemented age estimates based on external features with examination of internal growth features using thin transverse sections and light microscopy (Wilson 1984; Prince et al. 1986). However, Hill (1986) statistically compared age estimates using external and internal growth features and found no significant difference between the two methods. Therefore, age estimates reported in this study were based only upon examination of external features.

Vertebrae Analyses

Caudal vertebrae numbers 22 and 23 were removed from the area between the posterior portion of the second dorsal fin and the base of the caudal fin. These were the only vertebrae which could be removed without lowering the market value of the fish. Vertebrae were simmered for several hours in hot water to remove extraneous tissues and then air dried for at least 72 hours. Vertebral spines and arches were removed, anterior and posterior centra separated, cut longitudinally along the dorsoventral plane, and stored in 95% isopropyl alcohol.

Vertebral cone depth (CD) (as defined by Johnson 1983), referred to in this paper as centrum cone depth was measured to the nearest 0.05 mm. Growth rings were observed after carefully peeling away the thin layer of cartilaginous tissue which covers the bony face of the centra. Centrum length, from focus to outside edge, was divided into approximately 5 mm sections and the average number of rings per millimeter was calculated for each section by counting three 1 mm portions in each section. Total

increment number was extrapolated from these data.

Assessment of Ageing Techniques

The usefulness of each hardpart for estimating age in blue marlin was assessed by considering ease of collection, hardpart growth, precision of age estimates, and the legibility of each hardpart.

To test the hypothesis that hardpart growth was proportional to somatic growth of the animals, both LJFL and W were modeled with AR, DR, SW, and CD, categorized by sex. The significance (two-tailed test) of r^2 values was tested (Schefler 1979). A paradigm of the ageing theory is that the number of increments in or on a hardpart increases with the growth of the structure. To test this assumption, AR, DR, SW, and CD were modeled against increment counts for each structure and the significance of the r^2 values was tested.

Relative precision of age estimates and hardpart legibility were determined by comparing the variability of estimated ages between hardparts from the same fish. Direct comparisons of age estimates from corresponding hardparts (anal spines, dorsal spines, and sagittae) were modeled with linear regression, and the slopes of these regressions were tested to see if they varied significantly from parity (Ho: beta = 1; Zar 1984). The significance of correlation coefficients (r) of the comparisons was tested using methods outlined by Schefler (1979). These relationships were also tested using a Wilcoxon Signed Ranks test (Sokal and Rohlf 1981). Owing to the difference in increment types, vertebrae were not considered in these comparisons.

To test the consistency of age estimates within and between readers, a subsample of 20 of each hardpart was read three times each by two readers. Age estimates were compared using the Average Percent Error (APE) method of Beamish and Fournier (1981). Mean age estimates of each of these comparisons were compared using the Wilcoxon Signed Ranks test. Uncorrected anal and dorsal spine band counts were utilized for all reader comparisons.

RESULTS

Hardparts and morphometric data were taken from a total of 211 male and 105 female blue marlin. Males ranged in size from 114.8 cm LJFL (19.1 kg) to 263.1 cm LJFL (170.3 kg) and females from 147.0 cm LJFL (20.9 kg) to 445.8 cm LJFL (748.0 kg). The 263.1 cm LJFL male and the 445.8 cm LJFL female are the largest specimens of blue marlin from which biological data have been reported in the literature. The mean length of females (264.9 cm LJFL) was significantly greater than that of males (205.1 cm

TABLE 1.—Summary of numbers and size ranges of Pacific *Makaira nigricans* from which skeletal hardparts and measurements were collected. LJFL = lower jaw-fork length, AR = anal spine radius, DR = dorsal spine radius, SW = sagittal otolith weight, CD = centrum cone depth.

		LJFL (cm)			Weight (kg)			Hardpart size	
Hardpart	N	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
Anal spines								AR (mm):	
Males	150	114.8	263.1	205.3	19.1	170.3	75.0	3.98	10.10
Females	49	163.8	363.4	260.4	35.2	555.2	180.8	5.66	18.11
Dorsal spines								DR (mm):	
Males	66	177.0	263.1	208.7	46.3	170.3	78.5	7.65	12.46
Females	30	163.8	445.8	275.7	35.2	748.0	227.4	6.58	21.00
Otoliths								SW (mm):	
Males	54	169.5	251.5	206.4	38.6	138.8	75.9	0.415	4.985
Females	45	163.8	445.8	265.9	35.2	748.0	197.4	0.800	10.400
Vertebrae								CD (mm):	
Males	122	169.5	251.5	206.3	38.6	138.8	74.8	17.45	40.48
Females	77	147.0	337.7	261.1	20.9	447.7	176.5	18.30	45.99
Total									
Males		114.8	263.1	205.1	19.1	170.3	74.2		
Females		147.0	445.8	264.9	20.9	747.9	190.9		

LJFL) (Student's t-test; $P < 0.05$). Not all hardparts were collected from all fish. For a breakdown of fish size ranges and hardparts collected, the reader is referred to Table 1.

Hardpart Growth

The relationships between AR, DR, and CD, and LJFL were best described by significant ($P < 0.001$) positive linear equations (Table 2). Coefficient of determination values ranged from $r^2 = 0.19$ for male vertebrae to $r^2 = 0.72$ for female anal spines (Fig. 1). The relationships between SW and LJFL were exponential, with $r^2 = 0.41$ for males and $r^2 = 0.35$ for females (Table 2, Fig. 2). Logarithmic equations best described the relationships between AR, DR, CD, and W for both sexes (Table 2). Coefficient of determination values were significant ($P < 0.001$), ranging from $r^2 = 0.30$ for male vertebrae to $r^2 = 0.87$ for female dorsal spines. Sagitta weight had a linear relationship with W, with $r^2 = 0.32$ for males and $r^2 = 0.46$ for females.

Overall, there were generally higher coefficients of determination between AR, DR, CD, and W compared with those with LJFL. In addition, females generally had stronger relationships between hardpart size and body size (LJFL and W) when compared to males, the exception to this being the relationship between female SW and LJFL.

Growth Increments

Thin cross sections of dorsal and anal fin spines revealed a vascularized core matrix and a cortical region containing major growth bands (Fig. 3). A growth band was composed of alternations of translucent and opaque rings. Many growth bands were comprised of smaller rings that were most obvious at the widest lateral portion of the spine section (Fig. 4). Since band radii were measured from the focus outward along the widest portion of the spine, excessive numbers of smaller rings along the counting path made delineation of the outside edge of the translucent zone difficult at times, especially in exceptionally large spine samples. In such cases, it was necessary to refer to the dorsal and ven-

TABLE 2—Modeled relationships between fish growth (in length and weight) and hardpart growth for male and female Pacific *Makaira nigricans*. LJFL = lower jaw-fork length, W = roundweight, AR = anal spine radius, DR = dorsal spine radius, SW = sagitta weight, CD = centrum cone depth.

Comparison	Equation	r^2 value
Anal spine radius vs. LJFL		
Males	$AR = -0.5207 + 0.0394(LJFL)$	0.52
Females	$AR = -2.5879 + 0.0528(LJFL)$	0.72
Anal spine radius vs. W		
Males	$AR = 1.3061 * W^{0.4079}$	0.62
Females	$AR = 1.5300 * W^{0.3885}$	0.81
Dorsal spine radius vs. LJFL		
Males	$DR = -0.2700 + 0.0474(LJFL)$	0.49
Females	$DR = 0.2440 + 0.0526(LJFL)$	0.71
Dorsal spine radius vs. W		
Males	$DR = 2.0850 * W^{0.3513}$	0.53
Females	$DR = 2.3157 * W^{0.3499}$	0.87
Sagittal weight vs. LJFL		
Males	$SW = 0.0152 * 10^{(0.0103 * LJFL)}$	0.41
Females	$SW = 0.3250 * 10^{(0.0038 * LJFL)}$	0.35
Sagittal weight vs. W		
Males	$SW = -0.642 + 0.0412(W)$	0.32
Females	$SW = 1.1625 + 0.0144(W)$	0.46
Vertebral cone depth vs. LJFL		
Males	$CD = 2.5616 + 0.1226(LJFL)$	0.19
Females	$CD = 5.2871 + 0.1106(LJFL)$	0.45
Vetebral cone depth vs. W		
Males	$CD = 7.509 * W^{0.3031}$	0.30
Females	$CD = 10.101 * W^{0.2377}$	0.50

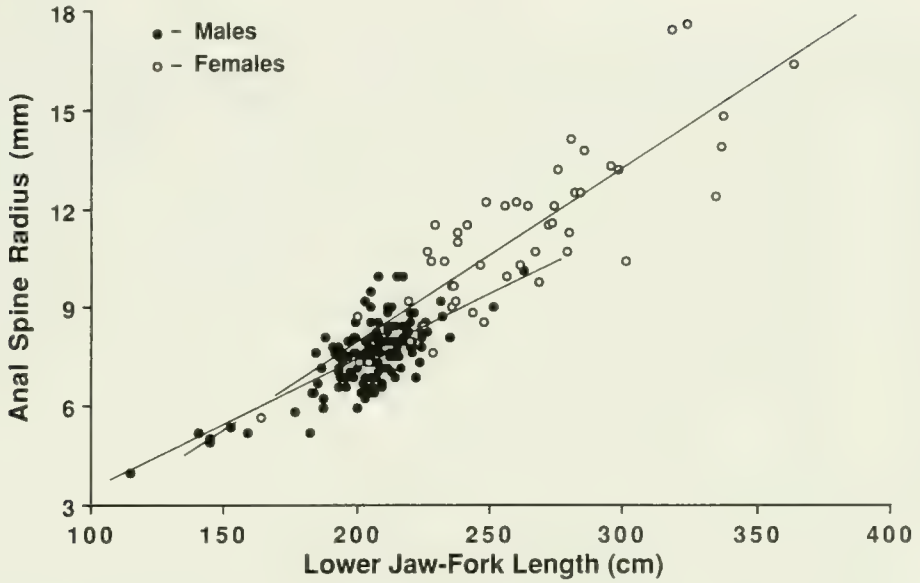


FIGURE 1.—Relationships between lower jaw-fork length (LJFL) and anal spine radius (AR) for male (n = 150) and female (n = 49) Pacific *Makaira nigricans*. Males: AR = −0.5207 + 0.0394 (LJFL) r^2 = 0.52; Females: AR = −2.5879 + 0.0528 (LJFL) r^2 = 0.72.

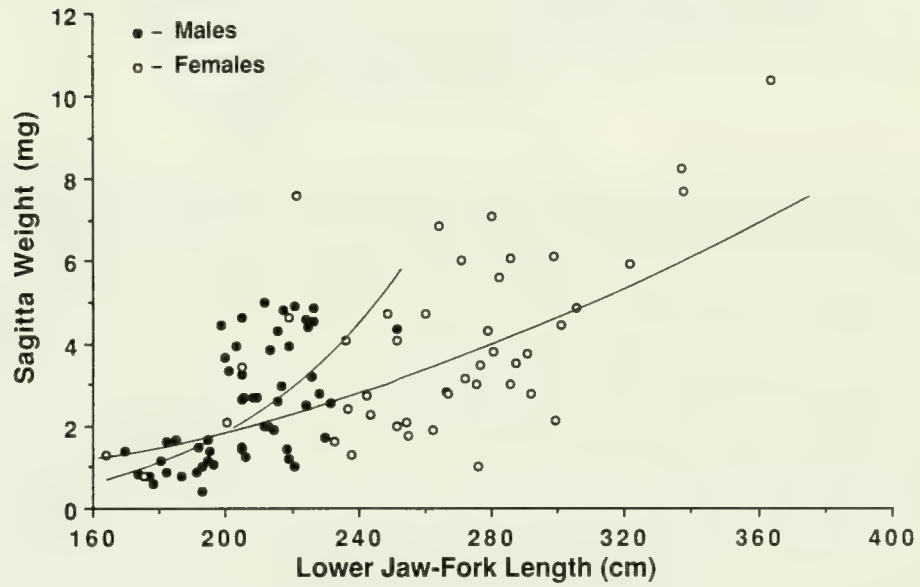


FIGURE 2.—Relationships between lower jaw-fork length (LJFL) and sagitta weight (SW) for male (n = 54) and female (n = 45) Pacific *Makaira nigricans*. Males: SW = 0.0152 * $10^{(0.0103 * \mathrm{LJFL})}$ r^2 = 0.41; Females: SW = 0.3250 * $10^{(0.0038 * \mathrm{LJFL})}$ r^2 = 0.35.

tral areas of the section where the bands were more compressed and clearly delineated. Anal spines were less compressed dorsoventrally than dorsal spines and this may have increased clarity of growth bands (Fig. 3).

Sagittae contained external features that suggested changes in structural growth rate over time. Growth of the rostrum was along two planes. Early growth occurred ventrally to the fish and increments were mainly comprised of

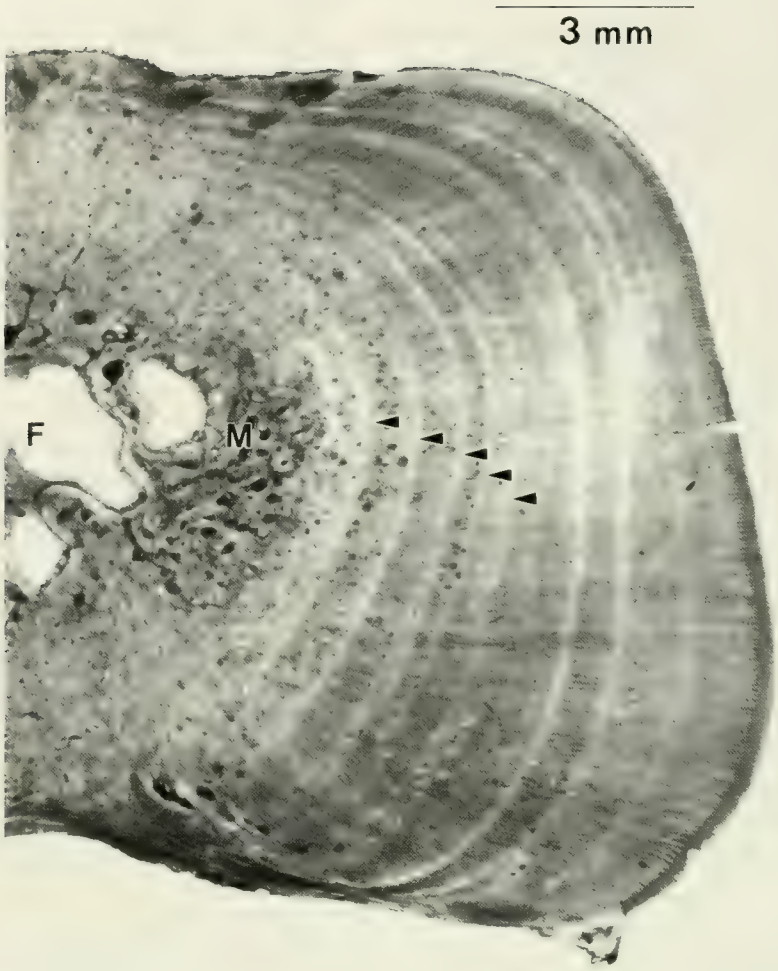


FIGURE 3.—Thin tranverse cross section of the 2nd anal spine from a 138.3 kg female Pacific *Makaira nigricans* as viewed by a binocular dissecting microscope at 63× magnification with transmitted light. Arrows indicate translucent edges of growth bands, F = focus; M = core matrix.

ridges along the anterior rostrum edge (Fig. 5). Between two and four ridges were counted along the anterior edge of the rostrum. Ridges were also visible along the ventral portion of the medial plane of growth (Fig. 6). Most sagittae had an excess of calcium carbonate which hindered ridge quantification to varying degrees (Fig. 6). Several sagittae were difficult to interpret owing to the mottled appearance of the rostrum face.

Vertebrae contained numerous minute (0.05–0.1 mm) concentric growth increments which were topographical features on the centrum face (Fig. 7). There were no prominent 3-dimensional features or changes in ring density which might be indicative of annular events.

Increment Counts and Hardpart Growth

Statistical replacement of early missing anal and dorsal spine bands in larger fish was accomplished by summarizing band radii statistics from smaller fish in which these early increments were visible (Fig. 4). Twenty-one percent of anal spines and 24% of dorsal spines had at least the first and second assumed annulus visible. There was no significant difference ($P <$

FIGURE 5.—Right sagitta from a 35.2 kg female Pacific *Makaira nigricans*. Arrows indicate prominences quantified for estimation of early lateral rostrum growth. R = rostrum; A = antirostrum; C = core region; p = posterior; a = anterior.

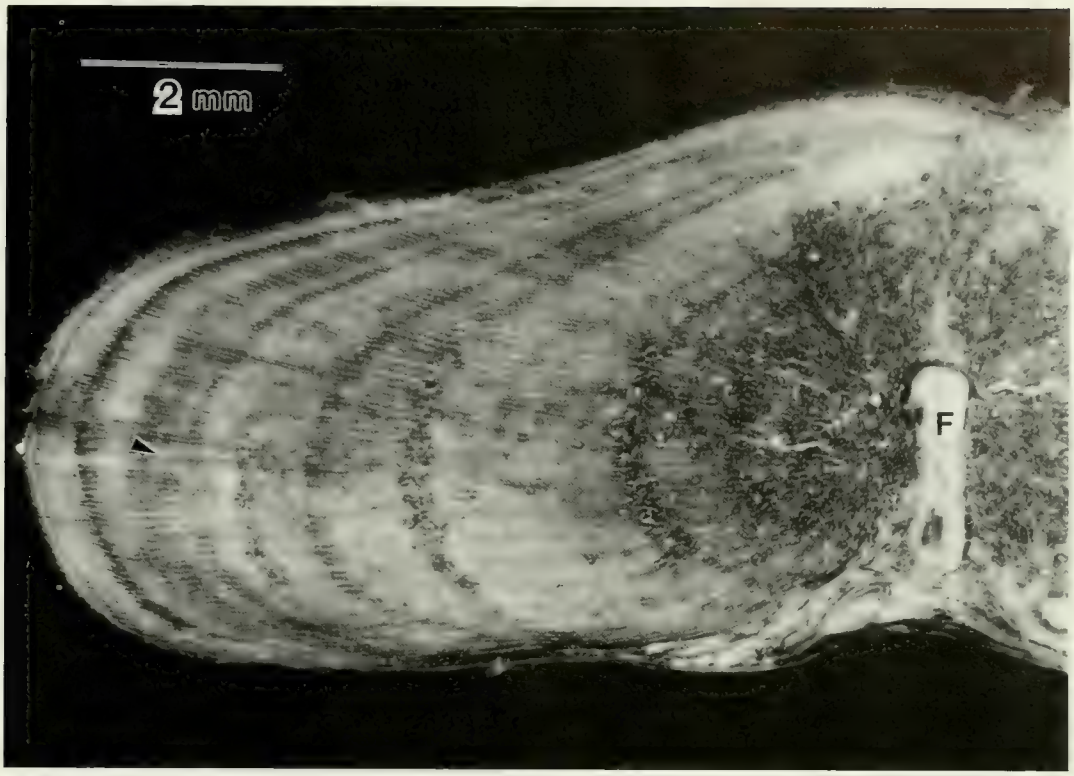
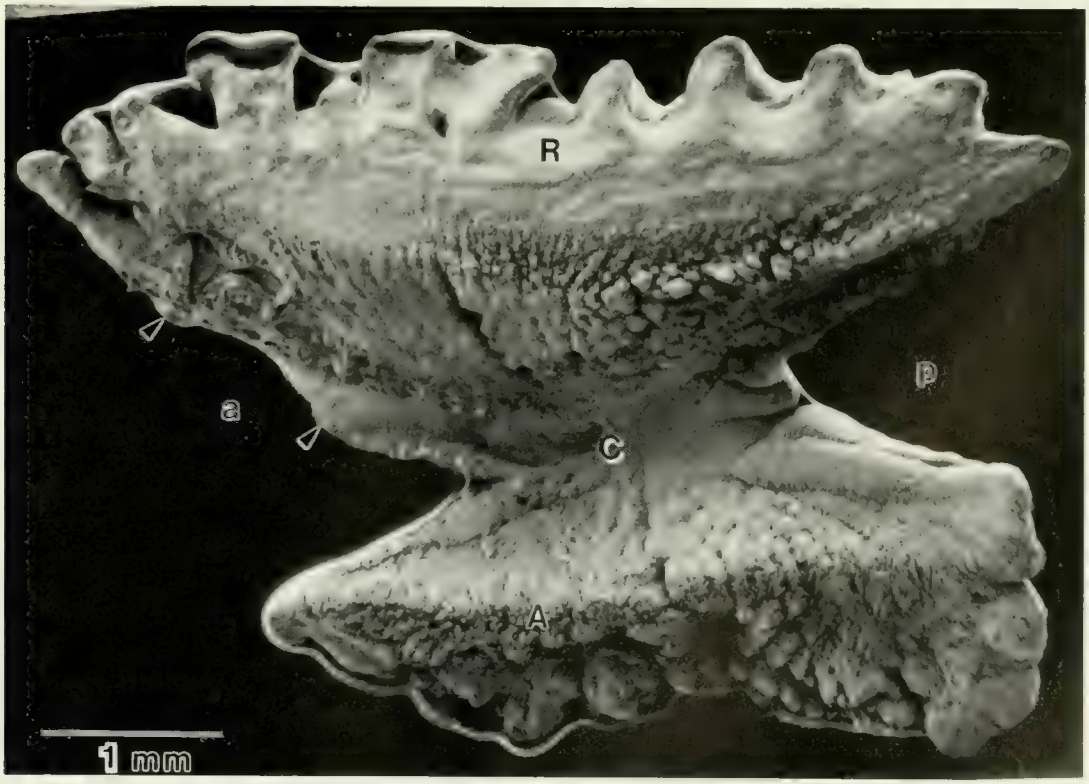


FIGURE 4.—Thin tranverse cross section of the 6th dorsal spine from a 52.4 kg male Pacific *Makaira nigricans* as viewed by a binocular dissecting microscope at 63× magnification with reflected light and a black background. F = focus. Arrow indicates area of multiple rings within a single growth band increment.



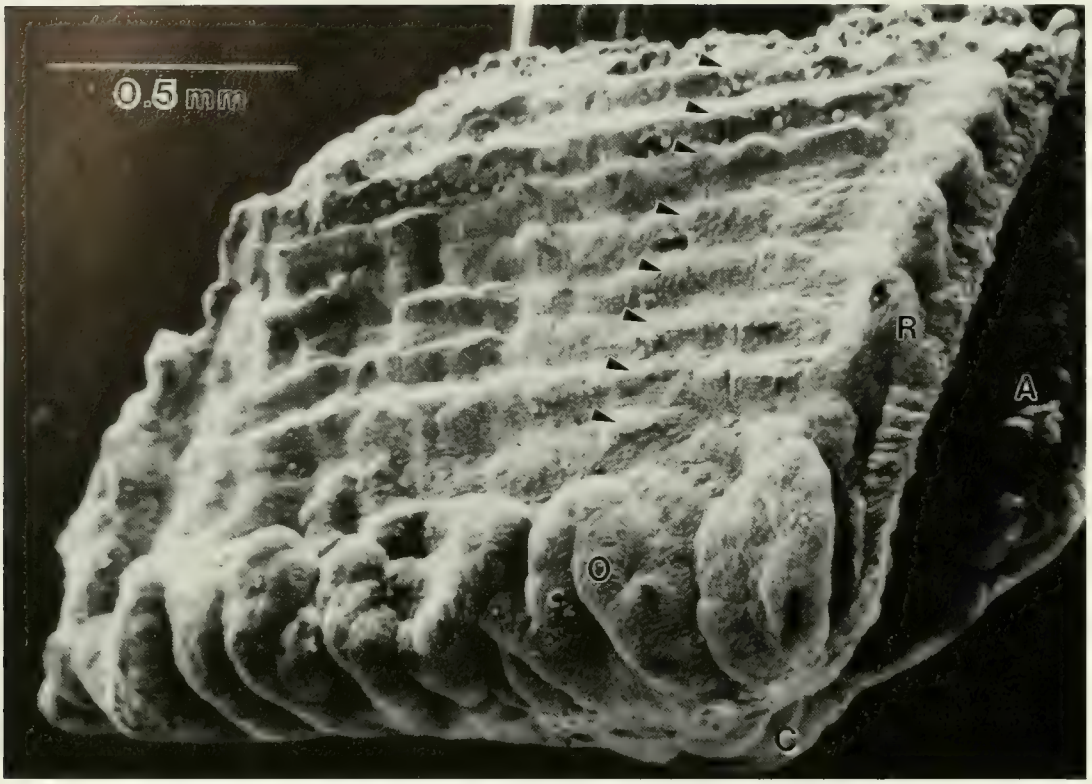


FIGURE 6.—Left sagitta from a 80.1 kg male Pacific *Makaira nigricans*. Arrows indicate rostral ridges quantified for age estimation. R = rostrum; A = antirostrum; C = core region; O = calcium carbonate overburden obscuring ridges.

0.01) between corresponding annuli for these two sets of data for either anal or dorsal spines; therefore, these two data sets were combined. There was, however, a significant difference in corresponding anal and dorsal spine band radii between males and females from the sixth band outward; therefore data were separated by sex (Fig. 8A, B).

Increment counts (sagitta ridges, corrected spine bands, and vertebral increments) increased with hardpart growth for each of the four structures considered. This relationship was logarithmic when increment counts were compared to AR, DR, and SW, and linear when compared to CD for both sexes (Table 3). Coefficients of determination were higher for females in all cases, and ranged from $r^2 = 0.39$ for male dorsal spines to $r^2 = 0.83$ for female dorsal spines.

TABLE 3—Modeled relationships between hardpart growth and increment counts for Pacific *Makaira nigricans*. LJFL = lower jaw-fork length, W = roundweight, AR = anal spine radius, DR = dorsal spine radius, SW = sagitta weight, CD = centrum cone depth, AC = corrected anal spine band counts, DC = corrected dorsal spine band counts, SC = sagittal ridge counts, VC = vertebral increment counts.

Comparison	Equation	r^2 value
Anal fin spines		
Males	$AC = 0.4521 * AR^{1.4316}$	0.62
Females	$AC = 0.5878 * AR^{1.2729}$	0.78
Dorsal fin spines		
Males	$DC = 0.9353 * DR^{1.0044}$	0.39
Females	$DC = 0.5380 * DR^{1.2227}$	0.83
Sagittal otoliths		
Males	$SW = 7.7206 * SW^{0.2941}$	0.41
Females	$SC = 7.1512 * SW^{0.4095}$	0.42
Vertebrae		
Males	$VC = 86.922 + 13.742(CD)$	0.56
Females	$VC = 59.115 + 15.311(CD)$	0.69

Hardpart Comparisons

There was a positive linear relationship between estimated counts of corrected growth in-

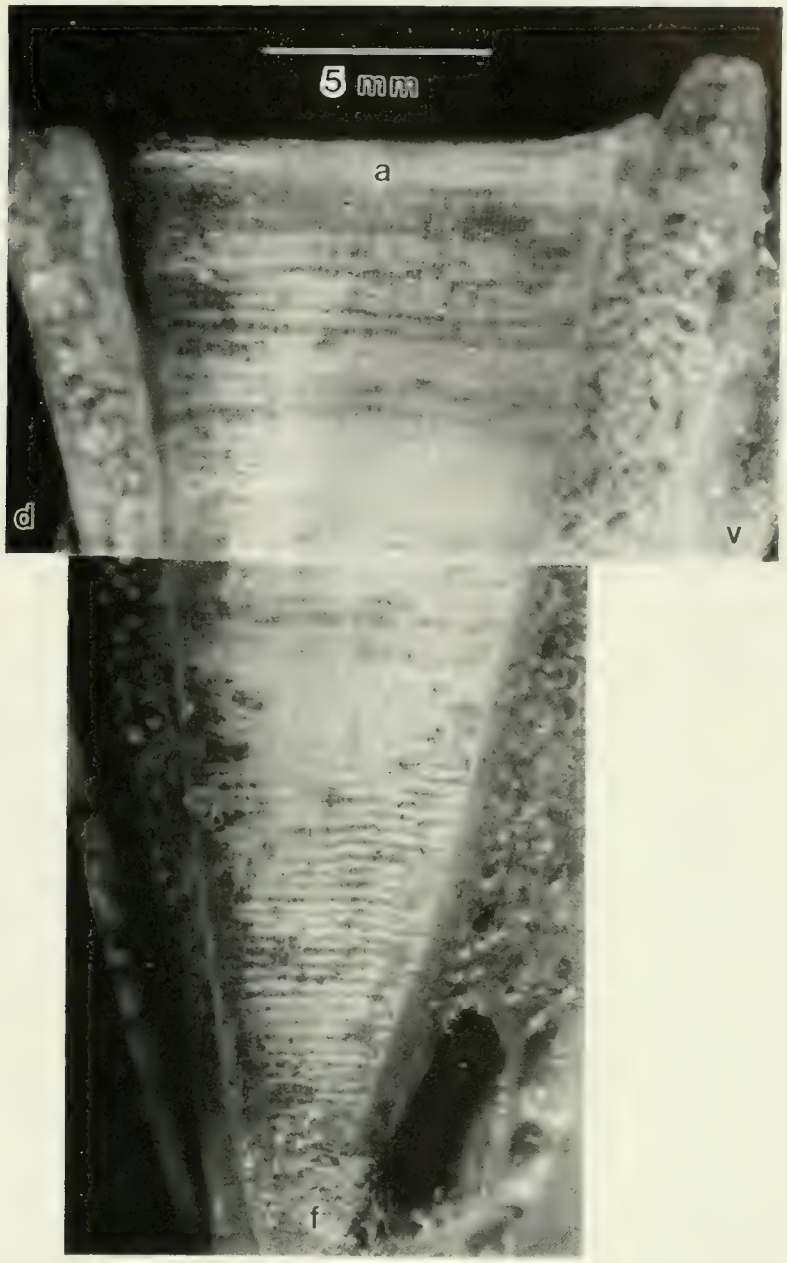


FIGURE 7.—Longitudinal cross section of the anterior centrum from the 23rd vertebrae from a 50.3 kg male Pacific *Makaira nigricans*. a = anterior end; d = dorsal; v = ventral; f = centrum focus.

crements in anal and dorsal spine sections and sagitta from the same blue marlin (Fig. 9A-C). The y-intercepts of these relationships were not significantly different from zero, and the slopes did not differ from parity (slope = 1; $P < 0.05$). Correlation coefficients ranged from $r = 0.84$ ($P < 0.001$) for anal spine and sagitta counts to $r = 0.95$ ($P < 0.001$) for the comparison of anal and dorsal spine counts. The greatest deviation in counts between corresponding hardparts was 9, where the anal spine count was 7 and the sagittal increment count was 16. Wilcoxon Signed Rank tests revealed no statistical difference between counts of these three structures ($P < 0.01$).

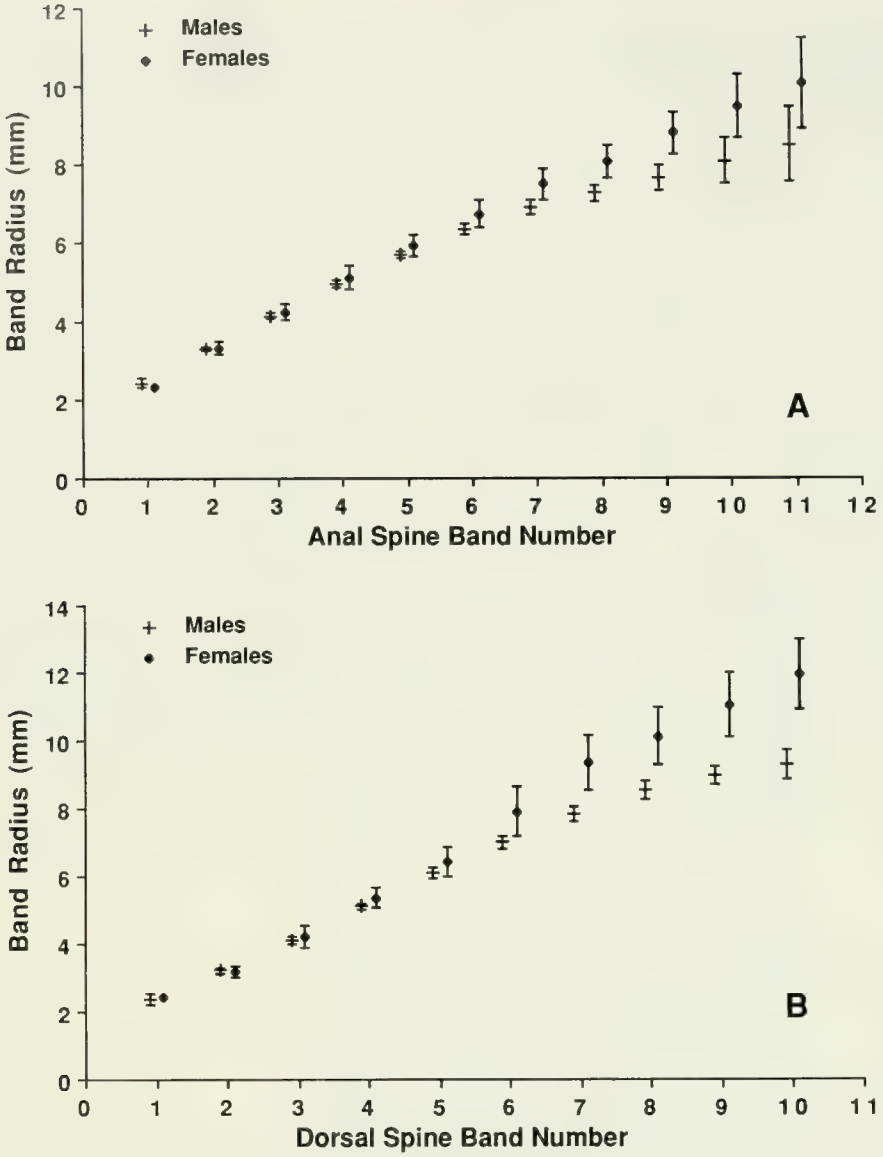


FIGURE 8.—Mean (±95% confidence limits) anal spine (A) and dorsal spine (B) band measurements for male and female Pacific *Makaira nigricans*. Data are from specimens that had at least the first or second band present. All other specimens were assigned inner rings and final age estimates based upon these data.

Reader Comparisons

Average Percent Error (APE) values ranged from 4.88% error for anal spines counted by reader 1 to 9.68% for sagittae counted by reader 2 (Table 4). Reader 1 had lower APE values (more precise age estimations) than reader 2 for each hardpart. Both readers had lowest APE values for anal spines and highest values for sagittae (Table 4).

Comparisons of differences (D) in mean age estimates between readers revealed that reader 1 had a tendency to give higher age estimates

TABLE 4—Average percent error (APE) values calculated from triplicate uncorrected readings of 20 randomly selected anal fin spines, dorsal fin spines, and sagittae.

	Average percent error results	
Hardpart	Reader 1	Reader 2
Anal fin spines	4.88%	8.79%
Dorsal fin spines	5.50%	9.18%
Sagittae	8.15%	9.68%

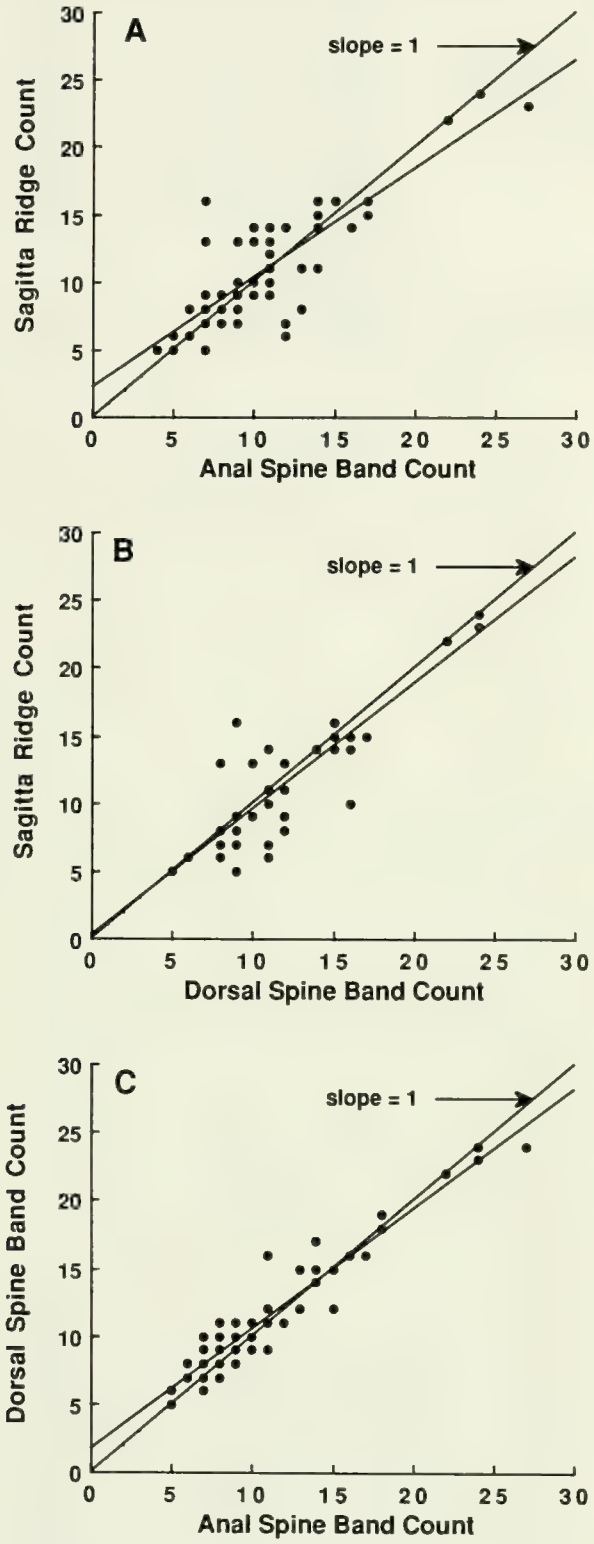


FIGURE 9.—Correlations between coresponding sagittal ridge counts (SC), corrected dorsal spine band counts (DC), and corrected anal spine band counts (AC) for male and female Pacific *Makaira nigricans*. Slopes of the regressions did not differ significantly from parity ($P < 0.05$). SC = 2.2905 + 0.8077(AC) $r = 0.84$; SC = 0.2069 + 0.9300(DC) $r = 0.86$; DC = 1.7682 + 0.8779(AC) $r = 0.95$.

than reader 2 for both anal (D = 0.85) and dorsal (D = 0.55) counts, while reader 2 assigned higher counts to otoliths (D = 1.5) (Fig. 10). None of these count differences differed significantly when compared with a Wilcoxon Signed Ranks test ($P < 0.05$). The greatest difference between mean counts was 8 for otoliths. Overall, there was a greater percentage of age estimates within ±1 and ± 2 years for anal and dorsal spines than for otoliths.

Mean Length at Estimated Age

Based on estimated ages from anal fin spines, there was a pronounced difference in growth between male and female marlin (Fig. 11). Males appear to grow to an average length of 202 cm LJFL at an estimated age of six years, after which growth is determinate. Growth of female marlin, more variable than males, is steady and does not level off as rapidly.

DISCUSSION

Growth patterns observed in dorsal and anal fin spine sections were similar to those described by Jolley (1977) for sailfish, Prince et al. (1984) for Atlantic blue and white marlin, and Wilson (1984) for Pacific blue marlin. Sagittal otolith morphologies were also similar to those from previous studies of Pacific blue marlin (Radtke 1981; Wilson 1984), and rostral ridges were analogous to those validated in one tag-recaptured sailfish specimen (Prince et al. 1986).

Three basic assumptions of the ageing theory are that 1) the growth of a structure used is proportional to growth of the animal, 2) the number of growth increments increase with the growth of the structure, and 3) the observed increments follow a discernible time scale e.g., one year of life (Bagenal 1974). In this study, growth of each hardpart was, to some degree, proportional to growth of the animal's length or weight. Increment counts increased with size of each hardpart, providing further support for the use of these structures for age estimation studies. With the exception of the comparison between SW and LJFL, females had higher coefficients of determination for the relationships between hardpart and somatic growth. This was probably due to the fact that a greater size range of females was sampled. The variable relationship between otolith weight and body size is not surprising since otoliths are so small, relative to

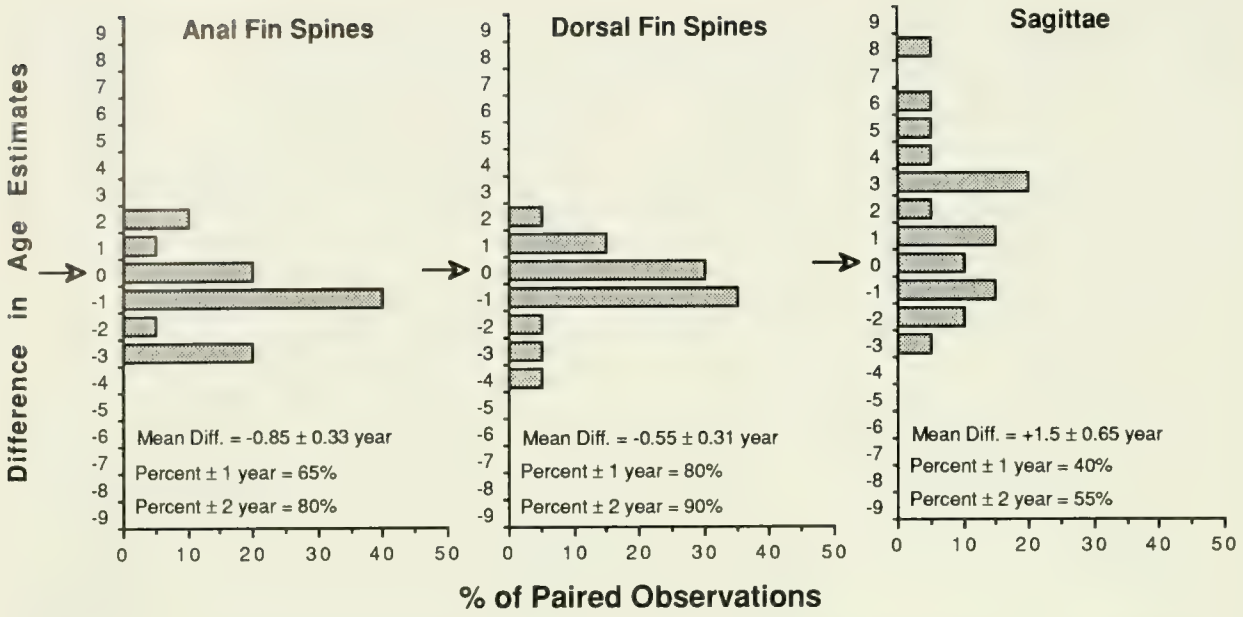


FIGURE 10.—Comparison of differences of mean age estimates between readers (1 minus 2) for anal spines, dorsal spines, and sagittae.

body size. It was expected that fin spines, much larger in size than otoliths, would have a closer relationship to body size. Prince et al. (1984) found a similar relationship between female and male size and hardpart growth for Atlantic blue marlin. The relationship between spine radius and body size may, therefore, be more useful than sagitta weight for back calculation of early growth in marlin. While the first two assumptions of ageing theory have been met, the most important assumption, that increments observed in spines and otoliths of blue marlin represent one calendar year of life, has yet to be proven.

While validation (or, confirmation of the temporal meaning of a growth increment) was not within the scope of this study, partial verification was achieved. Wilson et al. (1983) defined verification as "the confirmation of a numerical interpretation", usually used in reference to the precision of estimated age. Precision was determined by means of comparisons of age estimates from corresponding fin spines and sagittae as well as by means of measurement of error in age estimates within the data and between the data of both readers. In general, there was good agreement in age estimates between sagittae, anal spines, and dorsal spines from the same fish. Prince et al. (1984) described similar relationships between otoliths and dorsal spines of Atlantic blue and white marlin. While the variability of our counts between otoliths and their corresponding spines was greater than between corresponding spines, much of this variation was based on several cases in which the counts of sagittae were as much as 5–10 counts above or below those of corresponding spines. Neither the statistical tests of regression slopes nor the nonparametric tests were able to detect significant deviations from parity; these three structures may deposit increments in relation to similar environmental or growth stimuli.

Comparisons of age estimates, within the data and between the data of both readers provided information on the precision of each technique. Average percent error values of both reader estimates were lower for fin spines than for sagittae, which suggests that fin spine estimates produce a higher degree of precision than sagittae. Similarly, comparisons of differences in mean age estimates between readers revealed greater variability of age estimates resulted from sagittae compared to spines. Variability of sagittal age estimates may be due in part to problems involved with calcium overlayering, and the overlapping, successive ridges, or multiple smaller ridges on these structures. Wilson (1984) reported a similar individual variability in the general morphology and clarity of growth features of Atlantic blue marlin otoliths, and it is reasonable to assume that the interpretation of

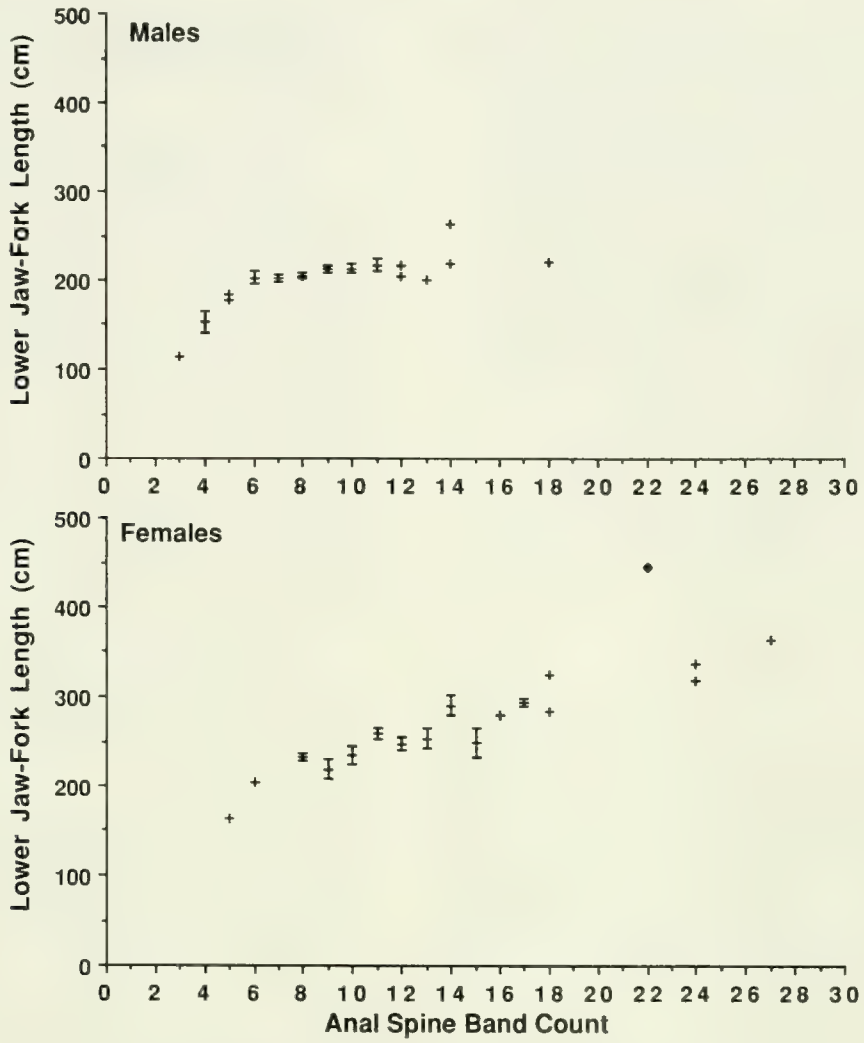


FIGURE 11.—Mean LJFL at age for male and female Pacific *Makaira nigricans* based on anal spine corrected band counts. Vertical lines terminated by narrow horizontal lines represent 95% confidence intervals (male n = 149; female n = 48). Closed diamond indicates estimated age of largest female sampled (748 kg) based upon dorsal spine and sagitta counts.

sagittal growth patterns is more subjective compared with the interpretation of spines.

Based on preliminary age estimates in this study, Pacific blue marlin males have a longevity of at least 18 years and females of at least 27 years of age. The largest female reported in this study was estimated to be 22 years of age based upon both dorsal spine and sagitta counts. The largest male sampled in this study (170.3 kg) was estimatd to be only 14 years of age and the oldest male (estimated age 18) was just above mean size. Wilson's (1984) study of Pacific blue marlin provided similar age estimates and sizes for each sex.

CONCLUSION

1) Anal fin spines, dorsal fin spines, and sagittal otoliths contained growth information which we assumed to be annual in nature and to hold promise for age estimation of this species. Incremental patterns in caudal vertebrae, possibly related to some other environmental or growth stimuli, were not useful for age estimation at this time.

2) Anal and dorsal fin spines are simpler to collect and process than sagittae, and to provide more precise (although not necessarily more accurate) age estimates for this species. The prob-

lem of early growth increment destruction by core matrix expansion can be partially overcome through application of band radius statistics; however, this technique may introduce bias to final age estimates. With the further compilation of band radius statistics and the application of techniques such as discriminate function analysis fin spine counts may also bring final age estimates closer to "true" age.

3) Sagittal otoliths are more difficult to collect and process and have more variable growth rates and morphologies than fin spines. While age estimates based on external features of sagittae are perhaps more subjective, sagittae may provide more detailed information from internal features such as "daily" increments, valuable for age estimation of young of the year.

4) Extensive mark/tag recapture studies are needed to validate the true meaning of the periodicities assumed to be annual.

ACKNOWLEDGMENT

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Age and Growth of the Blacktip Shark, *Carcharhinus limbatus*, near Tampa Bay, Florida

Kristie A. Killam and Glenn R. Parsons

ABSTRACT: Age and growth of the blacktip shark, *Carcharhinus limbatus*, was investigated in the Tampa Bay area of Florida during May 1985–February 1987. Two hundred and eighteen sharks were captured, and vertebrae were examined from 86 females (52.4–183.0 cm TL) and 54 males (59.8–160.5 cm TL). Minimum and maximum number of translucent winter rings was 0 and 11. Marginal increment analysis on juvenile blacktips with one to three translucent vertebral rings suggested an annual ring deposition during December–January. Length-frequency and length-month analyses suggested three age classes for blacktips <120 cm TL. Growth in length and percentage of size increase of blacktips age 0 and I was 21.0 (29.3%) and 19.0 (20.7%) cm/yr, respectively. Growth in weight and percentage of size increase of age 0 and I blacktips was 3.09 (120.7%) and 3.29 (58.2%) kg/yr, respectively. Age at maturity was 6–7 years (158–162 cm TL) for females and 4–5 years (133–136 cm TL) for males. Maximum age of blacktips captured was 10 years for two females 179.0 and 180.0 cm TL, and 9 years for a 160.5 cm TL male. Growth in weight was fit with a logistic equation. Von Bertalanffy growth parameters for females were estimated at L_∞ = 195.0 cm TL, k = 0.197 and t_0 = −1.154 years and for males, L_∞ = 166.5 cm TL, k = 0.276, and t_0 = −0.884 years.

Blacktip sharks, *Carcharhinus limbatus*, are distributed in all tropical and subtropical continental waters (Compagno 1984) and are very common inhabitants of inshore coastal and estuarine regions in Florida and the Gulf of Mexico (Springer 1940; Clark and von Schmidt 1965; Dodrill 1977; Branstetter 1981; Killam 1987). Recently, blacktip sharks have received commercial interest because of their increased value as a food fish. Commercial shark landings in Florida have risen steadily from 170,740 pounds in 1979 to 1,910,222 pounds in 1986 (Florida Department of Natural Resources 1979–86). In California a similar situation has occurred where landings for the common thresher shark, *Alopias vulpinus*, the blue shark, *Prionace glauca*, and the shortfin mako, *Isurus oxyrinchus*, increased from 800,000 pounds in 1976 to 3,500,000 pounds in 1981 (Cailliet and Bedford 1983).

Elasmobranch populations are thought to be easily overexploited because of their relatively slow growth rates, long gestation periods, and low fecundity (Holden 1974, 1977). As apex predators in complex estuarine and marine ecosystems, blacktip sharks have an important ecological role. Increased exploitation of blacktip shark stocks may effect lower trophic levels in the ecosystem, therefore sound life history information is needed. At present, little information is available concerning the biology of the blacktip shark. Its reproductive biology has been examined in the northern (Branstetter 1981) and east-central (Clark and von Schmidt 1965; Killam 1987) Gulf of Mexico. Killam (1987) provided detailed informaton on the seasonal distribution, reproductive biology, and feeding habits of *C. limbatus* captured near Tampa Bay, FL. Dodrill (1977) provided life history information on blacktip sharks captured along the east coast of Florida. Garrick (1982) reported that distinct populations of *C. limbatus* may exist in different geographic regions, because maximum attainable size and sizes at maturity differ markedly between regions.

At present only a single study has been completed concerning the age and growth of the blacktip shark. Branstetter (1987a) estimated growth parameters of *C. limbatus* in the northwestern Gulf of Mexico. This study provides additional information on the age and growth of *C. limbatus* by 1) providing a detailed examination of early growth rates using length-frequency and length-month analyses, 2) utilizing marginal increment analysis on juvenile *C. limbatus* to determine periodicity of ring deposition, and 3) identifying differences in age and growth rates between female and male *C. limbatus*.

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MATERIALS AND METHODS

Two hundred and eighteen blacktip sharks were collected in Tampa Bay and adjacent offshore areas during May 1985–February 1987. One hundred and forty were utilized for age and growth analyses. Sharks were caught with gill nets, longlines, and rod and reel. Once captured, total length (TL), fork length (FL), and precaudal length (PCL) were measured. Total length of embryos was measured with caudal fin extended horizontally. All lengths reported in this paper refer to total lengths. Sharks were then weighed and sexed. Maturity of males and females was determined using morphological and gonadal characteristics described by Clark and von Schmidt (1965) and Wass (1973).

A section of the vertebral column was removed just anterior to the first dorsal fin, although in a few instances only caudal vertebrae were obtainable. The vertebrae were stored frozen, then cleaned of connective tissue by soaking the individual centra in a solution of 5.25% sodium hypochlorite. Centra were then rinsed and stored in a solution of 70% ethanol. Two techniques were tested to determine optimum enhancement of translucent vertebral rings: the silver nitrate technique (Stevens 1975) was compared with a method described by Parsons (1983) in which the vertebral centrum face is shaded with a No. 1 pencil. The latter method detected differences in microtopography of the centrum face and enhanced the translucent rings. This method proved effective and was used because it took only a fraction of the time of the silver nitrate method. Vertebral centra were read under a dissecting microscope at 10× power using transmitted light. Centrum radius was measured from the focus to the dorsal margin using vernier calipers. Radii measurements were used to determine a relationship with shark TL. Ring radii were measured from the focus to each translucent ring, along the angle of the centrum (Fig. 1). Vertebrae collected from the caudal region were excluded from radius and marginal increment measurements. However, caudal vertebrae were utilized in age determinations since ring counts made on centra from different areas of the vertebral column resulted in similar age estimations. Translucent rings enhanced by the pencil method were counted if they extended continuously around the centrum face. Centra were read independently by the two authors. When discrepancies occurred, the vertebrae were reread until an agreement was reached. Ten centra were unreadable and were discarded from the analysis. Twenty centra of varying size were sectioned with a low speed saw through the focus, along the dorsal-ventral plane, for comparative ring counts with whole centra. Since blacktip sharks are born during late April through early June (Killam 1987), ages and growth rates were estimated based on an arbitrary 1 May birth date.

Back-calculated size at age was determined by a direct proportion method (Everhart and Youngs 1981):

$$(TL)_n = (TL)_c \times (VR)_n/(VR)_c$$

where TL_n = calculated length at ring n, TL_c = total length at capture, VR_c = the centrum radius at capture, and VR_n = centrum radius to ring n. Back-calculations were made on blacktip sharks of all sizes.

Marginal increment analysis examines the distance from the most recently deposited ring to the centrum margin and was utilized to determine the time of year that rings are deposited. The centrum margin becomes difficult to resolve in older fish and, therefore, only sharks with one, two, or three rings were utilized in this analysis. Marginal increments were measured from the distal most translucent ring to the edge of the centrum (Fig. 1). Measurements were made with vernier calipers along the angle of the centrum face.

Age and weight relationships were determined by fitting a logistic growth curve to observed data, as described by Kappenman (1981).

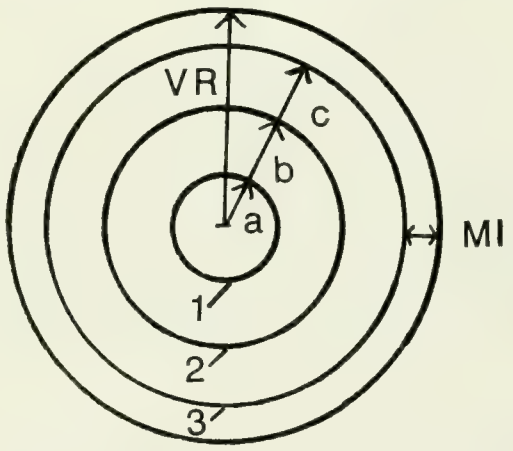

FIGURE 1.—Diagram of typical vertebral centrum of *Carcharhinus limbatus*. Measurements taken include: VR = vertebral radius; MI = marginal increment; a, b, and c = ring radii of translucent rings 1, 2, and 3. Measurements were taken along the dorsal-ventral plane.

The equation is

$$W = a/1 + \exp^{(-(b*r)+c)},$$

where W = weight in kg, a = asymptotic weight in kg, r = number of vertebral rings, and b and c are constants.

The von Bertalanffy (1938) growth equation was used to predict a growth curve for male and female blacktip sharks (Ricker 1975). The equation is

$$L_t = L_\infty(1 - \exp^{-K(t - t_0)}),$$

where L_t = length at age t in years, L_∞ = maximum theoretical length, K = the rate at which the asymptote is reached, and t_0 = the theoretical age at zero length. The von Bertalanffy growth equation was fit to observed data using a nonlinear, Statistical Analysis System method (SAS Institute, Inc. 1982).

RESULTS

Centrum Analysis

A total of 140 vertebral centra were read from 86 female and 54 male *C. limbatus*. These sharks ranged in size from 52.4 to 183.0 cm. The minimum and maximum numbers of translucent rings counted were 0 and 11. Centrum radii ranged from 2.8 to 10.6 mm. Initially, exact agreement of ring counts was reached on 83% of the readings, 15% differed by one ring, and 2% by two rings. Translucent ring counts made on sectioned centra were very similar to those of the corresponding whole centra. The number of translucent rings counted ranged from 1 through 10. When comparisons between whole and sectioned centra were made, exact agreement was reached on 15 centra, 3 centra differed by one ring and 2 centra differed by two rings. In addition, the ring structures counted on the sectioned centra were coincidental with those enhanced by the pencil method. Subjectivity is involved in both methods and sometimes resulted in slightly different counts.

The relationship between blacktip shark total length and centrum radius was linear for both sexes. Analysis of covariance (ANCOVA) indicated no significant difference in the regression lines between sexes, so data were combined into the relationship (Fig. 2)

$$TL = 63.2 + (16.7)R \qquad (r = 0.9797, N = 130)$$

where TL = total length in mm and R = centrum radius in mm.

Initial vertebral ring deposition appeared to occur at or shortly after parturition. Examination of 15 centra from embryonic *C. limbatus*, which ranged in size from 48.4 to 61.8 cm, had no observable translucent ring formation. These sharks were collected between April and June 1986. If a ring had been deposited prior to birth, it should have been visible in the near-term embryos. Free-swimming juveniles captured in late May and early June had a translucent ring deposited on the edge of the centrum. With subsequent growth, this "birth" ring became more apparent as opaque tissue was deposited distally to it.

Marginal increment data on juvenile blacktip sharks (52.4–116.0 cm) of both sexes were combined, because at this age there were no significant differences in sizes (Student's t-test, $P > 0.10$). Fish captured in early February were approximately 9 months old and had very small marginal increments (0.1–0.2 mm), indicating recent ring deposition. Analysis of juveniles taken later in the spring and summer showed that marginal increments increased in width (Fig. 3) to as much as 1.4 mm until December when the next ring formed. This analysis suggests ring deposition occurs during the months of December–January and, in the juvenile blacktip shark, is an annual event.

Early Growth Rates

The relatively large numbers of juvenile and subadult blacktip sharks examined in this study allowed the estimation of early growth rates. A length-frequency distribution of sharks <120 cm TL captured during the months of May–August suggests three separate size classes at approximately 68, 93, and 111 cm (Fig. 4). A length-month distribution (Fig. 5) indicated three distinct size classes for juvenile blacktip sharks <120 cm, and these fish appeared to represent three separate cohorts. Rapid growth of the young sharks produced distinct separations in length and weight between these age classes (Table 1) and each of the sharks examined from these three age classes had one, two, or three translucent rings, respectively. This further supports the annual nature of vertebral ring deposition in juvenile blacktip sharks.

Growth of neonatal sharks was found to be rapid. Mean size of free-swimming juveniles captured during June was 60.5 cm (SD = 3.9, N =

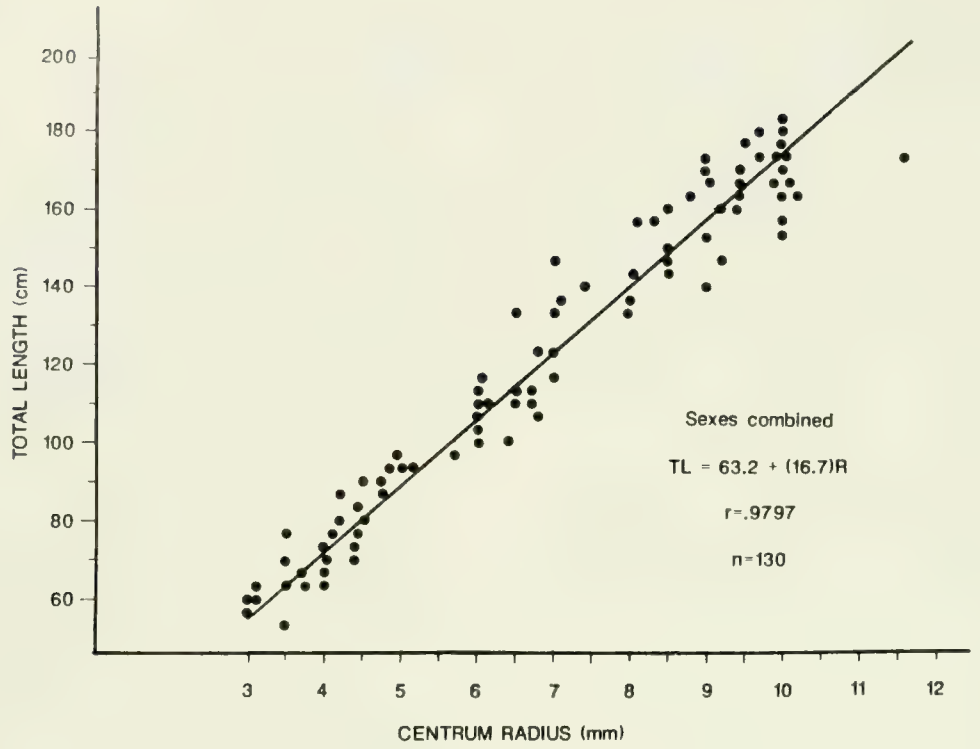

FIGURE 2.—Relationship between vertebral centrum radius and total length (sexes combined) for blacktip sharks captured in the Tampa Bay area of Florida.

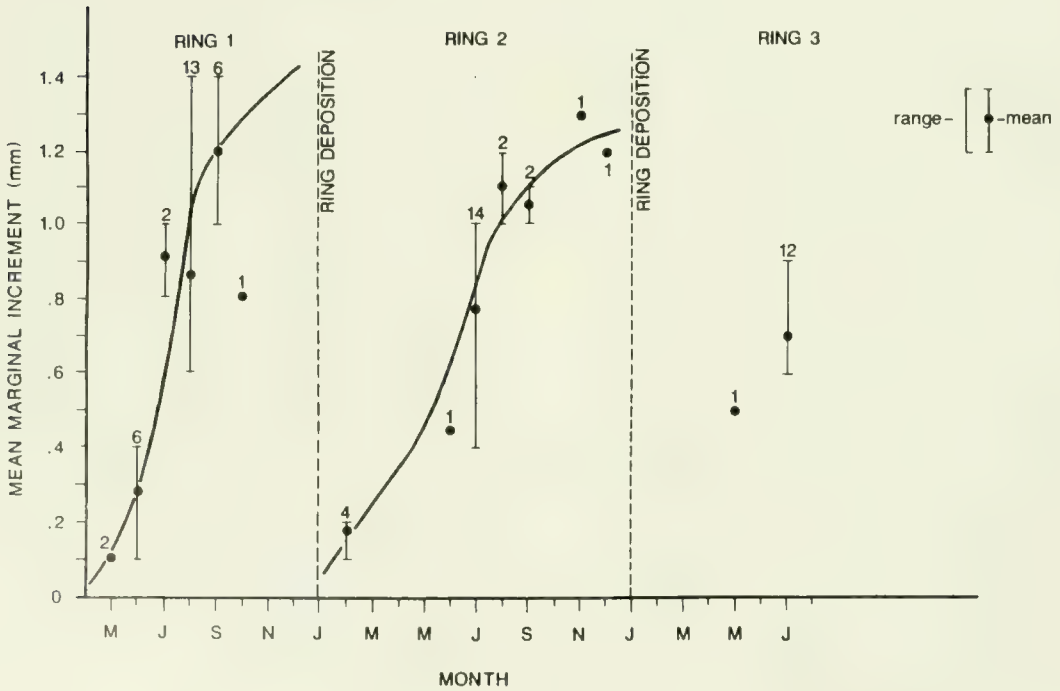

FIGURE 3.—Mean monthly marginal increment correlated with month of capture for blacktip sharks with 1, 2, or 3 vertebral rings. Curves were fit by eye to best approximate the seasonal increase in marginal increment. Translucent ring deposition appears to occur during December or January.

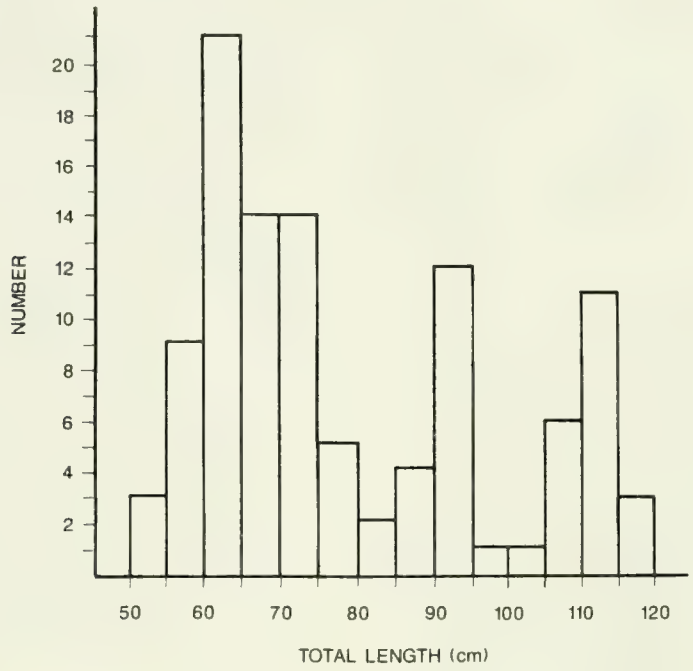

FIGURE 4.—Length-frequency distribution of juvenile blacktip sharks <120 cm TL. Three peaks in abundance are apparent and probably indicative of separate age classes.

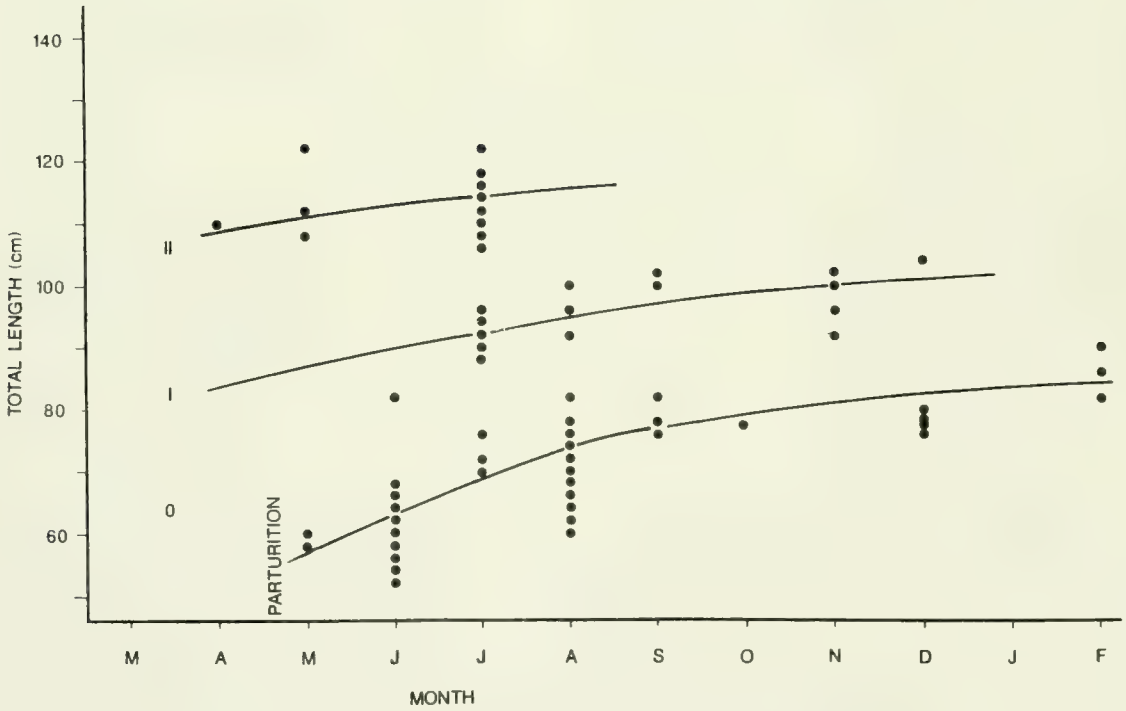

FIGURE 5.—A length-month distribution for juvenile blacktip sharks in age classes 0–II. Curve was fit by eye to best approximate the seasonal increase in total length for each age class.

TABLE 1.—Size differences among juvenile blacktip sharks with 1, 2, or 3 vertebral rings, captured during July and August 1986.

No. rings	No. fish	Mean TL (cm) ± SD	Mean weight (kg) ± SD
1	14	68.7 ± 1.2	2.3 ± 1.2
2	15	93.2 ± 7.3	5.8 ± 1.6
3	15	111.4 ± 8.5	8.9 ± 2.3

33) and mean weight was 1.47 kg (SD = 0.28, N = 29). These fish had prominent umbilical scars which indicated recent parturition. Sharks of this size possessed a birth ring on their vertebral centra and were assigned to age class 0. By mid–August, age 0 sharks had increased 11.1 cm (mean TL = 71.6 cm, SD = 4.74, N = 28), and 1.09 kg (mean weight = 2.56 kg, SD = 0.46, N = 28). This is an increase in length of 18.3% and an increase in weight of 74.0% from mid–June to mid–August. Growth during the first two months was 5.56 cm and 0.55 kg/mo. Four age class 0 *C. limbatus* captured in early February possessed two vertebral rings on their centra and had a mean TL of 85.5 cm (SD = 2.3, N = 4). Compared with the lengths of age 0 fish in mid–August, these fish had grown an additional 13.9 cm or approximately 2.5 cm/mo. This indicates a decline in growth rates over the winter months, and is depicted as a leveling off of the growth curves on the length-month distribution (Fig. 5).

Blacktip sharks captured after May 1 that possessed two vertebral rings (a birth ring and a first winter ring) were assigned to age class I. In late July, these fish had a mean length of 92.6 cm (SD = 2.36, N = 13) and mean weight of 5.65 kg (SD = 0.84, N = 14) representing growth in one year of approximately 21.0 cm (29.3%) and 3.09 kg (120.7%). Age class II sharks (3 vertebral rings) captured in late July had a mean length of 111.8 cm (SD = 3.51, N = 15) and a mean weight of 8.94 kg (SD = 0.80, N = 13) representing an increase of 19.2 cm (20.7%) and 3.29 kg (58.2%) in their second year of growth.

Age-Length

Growth in length was described using the von

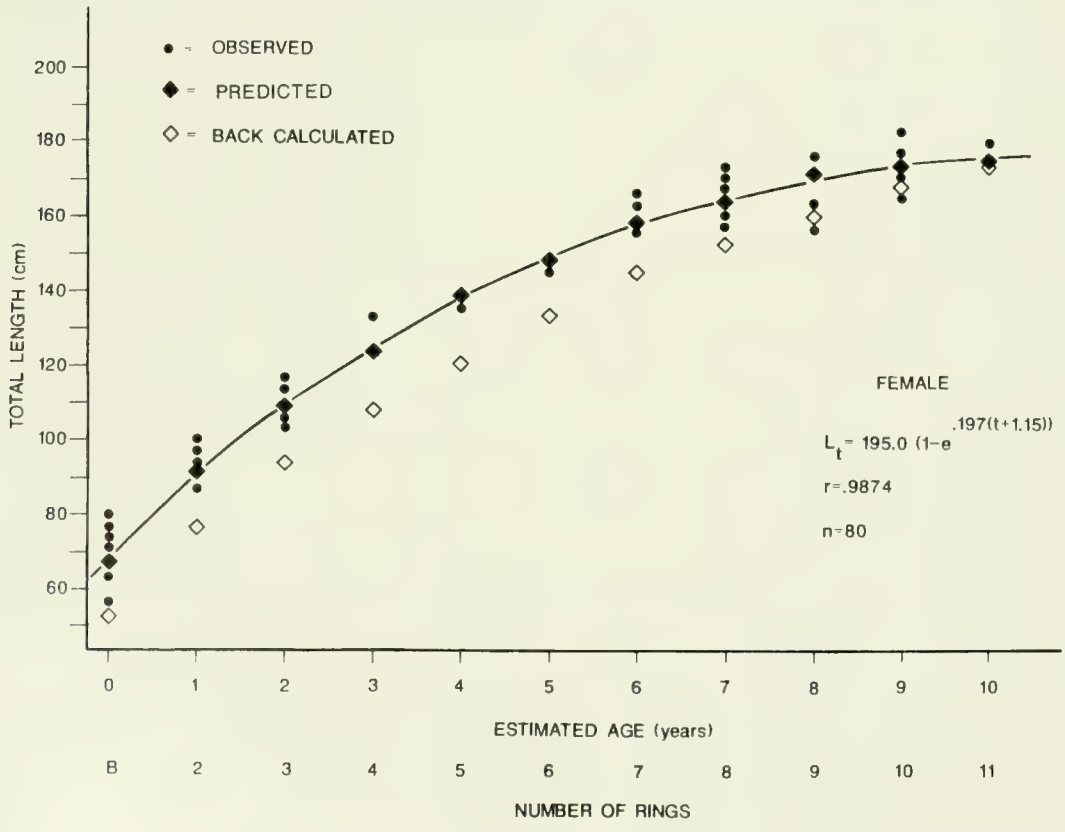

FIGURE 6.—Von Bertalanffy growth curve for female blacktip sharks fit from observed data. Distance between ring B and ring 1 is only 7–8 months but is represented as a 1-yr interval to prevent overestimation of early growth rates.

Bertalanffy growth equation fit with observed data. Growth curves for both sexes were significant at $P < 0.05$. Growth equations produced for female and male *C. limbatus* were

$$\text{Female: } L_t = 195.0\,(1 - \exp^{0.197(t+1.15)})$$
$$r = 0.987,\ N = 80$$

$$\text{Male: } L_t = 166.5\,(1 - \exp^{0.276(t+0.88)})$$
$$r = 0.979,\ N = 53.$$

Estimated maximum total length of females was significantly different from males as indicated by the separation of the calculated 95% confidence intervals. K values, although larger for males, were not significantly different from females (Table 2); however, females were significantly larger than males after age seven (Student's t-test, $P < 0.05$).

Growth rates for juvenile, adolescent, and mature blacktip sharks were approximately 19–21, 9–10, and 3–4 cm/yr, respectively. Females matured at 158–162 cm at 6–7 years; males matured at 133–136 cm at 4–5 years (Killam 1987, Figs. 6, 7). The smallest gravid female captured was six years old. Maximum age obtained by female *C. limbatus* was 10 years for two fish which measured 179.0 and 180.0 cm. Maximum age of male *C. limbatus* was nine years for a fish which measured 160.5 cm.

TABLE 2.—Estimated parameters of the von Bertalanffy growth equation derived using SAS nonlinear method, including 95% confidence intervals.

		Asymptotic 95% confidence interval	
Parameter	Estimate	Lower	Upper
Females			
L_∞(cm)	195.0	183.0	206.9
K	0.1967	0.1546	0.2393
t_0(yr)	−1.154	−1.555	−0.753
Males			
L_∞(cm)	166.5	155.0	177.9
K	0.2758	0.2066	0.3450
t_0(yr)	−0.8836	−1.3006	−0.4665

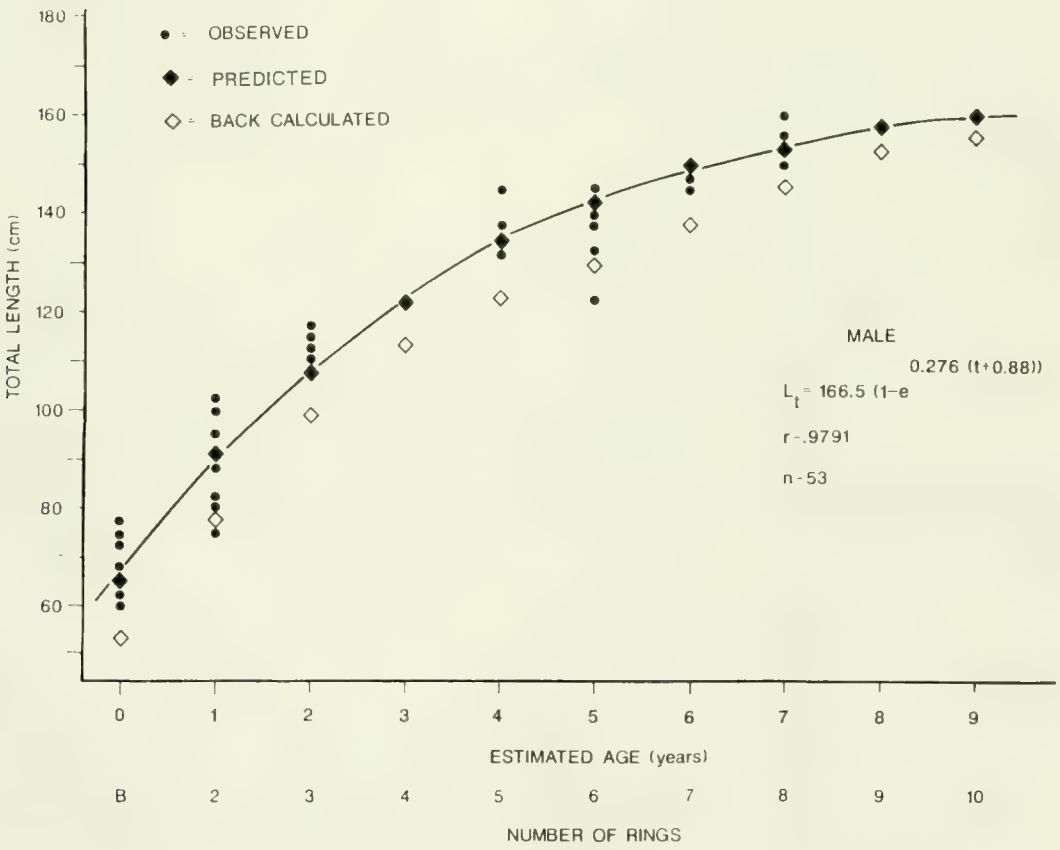

FIGURE 7.—Von Bertalanffy growth curve for male blacktip sharks fit from observed data. Distance between ring B and ring 1 is only 7–8 months but is represented as a 1-yr interval to prevent overestimation of early growth rates.

Back-Calculation

Back-calculated size at time of first ring deposition was 52.1 and 53.2 cm for females and males, respectively. These values correspond closely to observed sizes of *C. limbatus* at birth, further supporting the first translucent ring being a birth ring. Back-calculated size was inspected for "Lee's Phenomenon," which appeared to occur at some ages; however, no consistent trend was identified (Table 3). Mean back-calculated size at age was consistently lower than observed and predicted data (Figs. 6, 7).

Growth curves for both sexes were derived using observed data from sharks with 1–11 vertebral rings. As shown in Figures 6 and 7, ring 1 (birth ring) and ring 2 are shown to be one year apart. In actuality, the second translucent ring is deposited approximately 7–8 months after the formation of the birth ring. However, because 83.4% of these sharks were captured during the summer months of May–September, sharks with two translucent rings are more likely to be at least one year older than those with only the birth ring.

Age-Weight

The nonlinear relationship between shark age and weight was significantly fit with a logistic growth equation ($P < 0.05$). The relationship for females $(W)_f$ and males $(W)_m$ was

$$(W)_f = 42.68/1 + \exp^{-(0.540*r)-3.14}$$
$$r = 0.962, N = 69$$

$$(W)_m = 27.83/1 + \exp^{-(0.550*r)-2.58}$$
$$r = 0.974, N = 48$$

where W = weight in kg, and r = number of translucent rings (Figs. 8, 9). Growth in length and weight of *C. limbatus* appears to reach an asymptote, and blacktips greater than 10 years old probably grow very little each year.

TABLE 3.—Mean back-calculated total lengths (cm) at age, for female and male blacktip sharks captured in the Tampa Bay area of Florida.

Rings	Number	Mean	±	SE	B	1	2	3	4	5	6	7	8	9	10
Females															
B	19	68.1	±	8.0	54.3										
2	16	88.7	±	7.5	54.6	79.6									
3	5	109.7	±	4.1	49.2	77.6	101.0								
4	1	132.0	±		57.2	88.0	114.4	125.9							
5	1	136.4	±		49.9	68.2	96.5	113.1	126.4						
6	2	142.0	±	7.2	51.5	70.2	87.9	104.8	119.8	133.0					
7	2	157.0	±	10.1	50.9	69.9	88.0	103.6	119.2	133.9	144.2				
8	12	165.8	±	6.2	48.7	72.6	96.1	111.9	126.9	138.2	149.9	159.5			
9	6	166.4	±	8.0	48.5	66.8	85.4	100.7	114.1	127.0	137.9	138.8	158.6		
10	3	172.3	±	4.9	48.9	68.7	86.9	102.2	116.0	128.6	139.1	150.6	162.7	168.8	
11	2	179.1	±	7.6	51.0	69.9	87.9	103.1	119.3	131.0	140.8	149.8	157.9	170.3	176.5
Weighted mean					52.0	74.3	93.2	107.4	121.4	133.5	144.5	154.7	159.6	169.4	176.5
Number of back-calculations					69	50	34	29	28	27	25	23	11	5	2
Growth increment					22.6	18.9	14.2	14.0	12.1	11.0	10.2	4.9	9.8	7.1	
Males															
B	16	68.0	±	6.9	55.5										
2	12	89.4	±	8.7	53.0	79.7									
3	9	112.3	±	3.5	50.5	76.9	101.1								
4	1	122.0	±		56.1	79.4	103.6	125.6							
5	3	138.3	±	5.4	52.9	75.8	97.3	117.3	130.4						
6	3	135.7	±	8.8	51.1	75.5	95.3	109.0	120.3	132.8					
7	2	145.8	±	10.6	53.7	76.7	96.6	111.2	119.5	128.7	140.2				
8	1	155.1	±	5.4	51.7	72.4	93.1	110.3	120.7	132.8	141.4	148.3			
9	2	155.8	±	3.9	52.2	75.7	89.6	103.6	118.4	127.1	137.5	144.4	151.4		
10	1	160.5	±		46.7	63.8	95.0	110.6	118.4	126.2	134.0	140.0	148.0	154.3	
Weighted mean					53.2	77.2	97.8	112.0	122.3	129.9	138.4	144.2	150.3	154.3	
Number of back-calculations					50	34	22	13	12	9	6	4	3	1	
Growth increment					24.0	20.6	14.2	9.4	7.6	8.5	5.8	6.1	4.5		

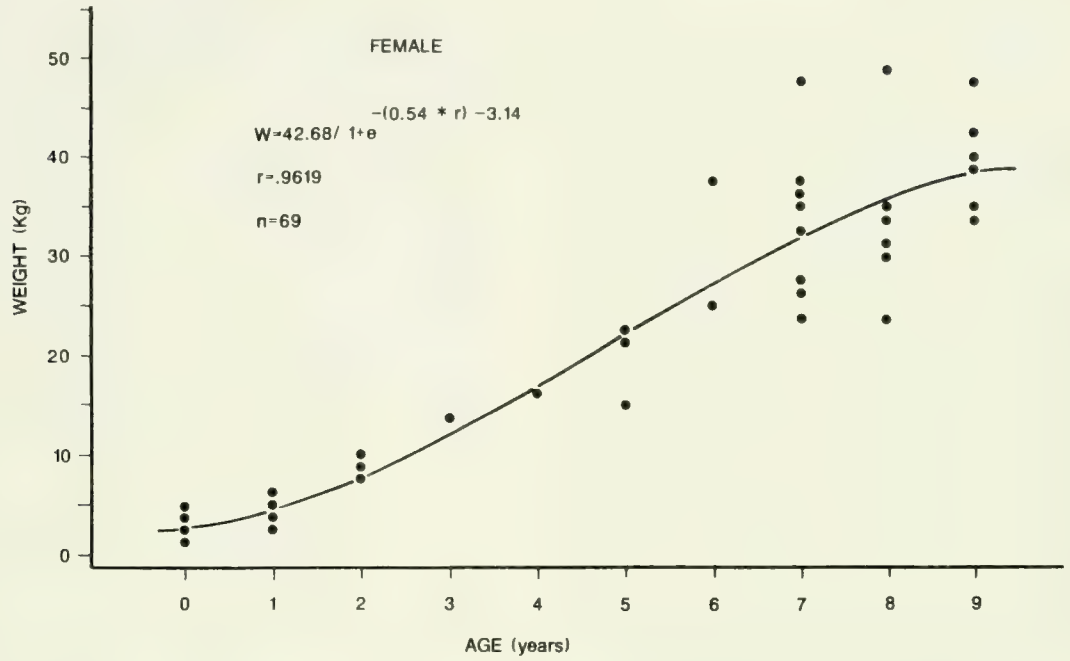

FIGURE 8.—Age-weight relationship for female blacktip sharks; logistic growth equation provided a significant fit to the data ($P < 0.05$).

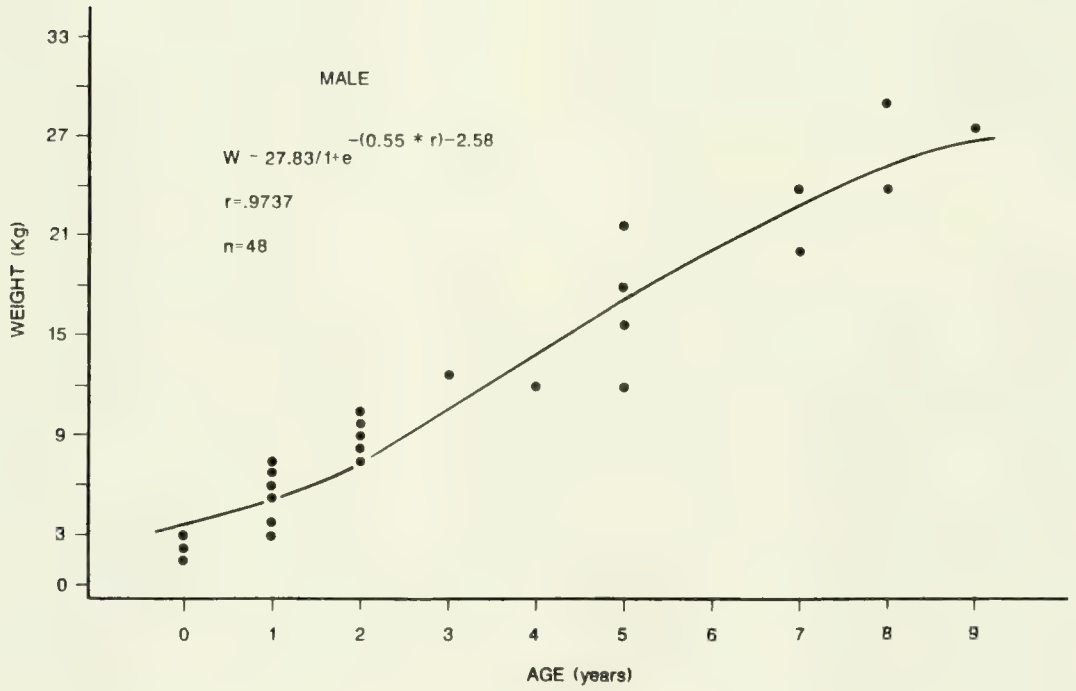

FIGURE 9.—Age-weight relationship for male blacktip sharks; logistic growth equation provided a significant fit to the data ($P < 0.05$).

DISCUSSION

Centrum analysis

Perhaps the most common limiting factor in many studies concerning shark species is the acquisition of sufficient specimens over the entire size range of the species. The relatively large sample size reported here made annulus verification and subsequent growth estimation possible. Marginal increment, length-frequency, and length-month analysis suggest that ring periodicity in juvenile *C. limbatus* is annual. Annual ring deposition in sharks has been verified or validated for several species, including *Prionace glauca* (Stevens 1975), *Rhizoprionodon terraenovae* (Parsons 1983), *Negaprion brevirostris* (Gruber and Stout 1983), *C. amblyrhynchos* (Radtke and Cailliet 1984), *Triakis semifasciata* (Smith 1984), *C. plumbeus* (Casey et al. 1985), *C. leucas* (Branstetter and Stiles 1987), *C. falciformis* and *Sphyrna lewini* (Branstetter 1987b), *Galeocerdo cuvieri* Branstetter et al. 1987), and *S. tiburo* (Parsons 1987). Cailliet et al. (1986) provided an extensive review of elasmobranch species for which age and growth rates have been estimated. In some lamnoid species such as *I. oxyrinchus* (Pratt and Casey 1983) and *Cetorhinus maximus* (Parker and Stott 1965), deposition of two rings per year has been suggested. Therefore, it appears that for each species being examined, periodicity of ring deposition must be verified or validated before proper age and growth estimates can be attained.

Early Growth

Because Tampa Bay is a nursery area for *Carcharhinus limbatus* (Killam 1987) the capture of numerous juvenile specimens was fairly easy. Rapid early growth rates of these young sharks made determination of periodicity of ring deposition possible. Marginal increment analysis suggested that one translucent ring is deposited during the winter months of December–January, and that opaque tissue is deposited distally to these rings, during periods of rapid growth in warmer months. A similar pattern of ring deposition has been identified in *C. amblyrhynchos* (Radtke and Cailliet 1984; Cailliet et al. 1986). The opaque areas have been found to contain higher amounts of calcium and phosphorus than the adjacent translucent rings.

The rapid early growth of juvenile *C. limbatus* produced distinct separations in length-frequency modes for sharks <120 cm TL. Modes are more difficult to resolve in larger *C. limbatus* because fish of similar sizes may represent a variety of age classes owing to differences in individual growth rates and the decrease in growth rate as age increases. Ketchen (1975) utilized length-frequency analysis to estimate early age classes of *Squalus acanthias*, 44–70 cm TL. It appears that only early age classes of sharks undergoing rapid growth can be estimated by analyzing length-frequency distributions. Casey et al. (1985) found that in 3–8 year old *C. plumbeus*, several age classes may be represented at any one length.

A length-month distribution subjectively assigned *C. limbatus* to age classes and provided estimates of growth rates. Modes identified by this method were subjectively assigned to age classes. Three age classes were apparent for blacktips 62–118 cm. As with the length-frequency distributions, the length-month distribution becomes increasingly difficult to resolve in older sharks. Pratt and Casey (1983) utilized this method to estimate three age classes of juvenile *I. oxyrinchus*, 54–175 cm TL. Parsons (1985) used this procedure to estimate age and growth through maturity for the rapidly growing *R. terraenovae* whose males mature as early as 2.0–2.4 years and females mature at 2.4–2.8 years.

Early growth rates have been examined in only a few species of sharks. Juvenile *C. leucas* grew at 18 and 16 cm/yr during the first 2 years, respectively, decreasing to 11 cm/yr in larger sharks (Thorson and Lacy 1982). *Rhizoprionodon terraenovae* growth rates for age classes 0 and I were 30 and 10 cm, respectively, which corresponded to a 100% increase in length for age 0 individuals and a 15% increase at age I (Parsons 1983). Young *N. brevirostris* growth rates did not exceed 25 cm/yr and probably averaged 10–20 cm/yr (Gruber and Stout 1983). *Galeocerdo cuvieri* appeared to grow > 20 cm/yr until near maturity (Branstetter et al. 1987). *Carcharhinus limbatus* had growth rates of 21.0 and 19.2 cm/yr for age classes 0 and I. A very similar growth rate was determined for juvenile *C. limbatus* in the northern Gulf of Mexico (Branstetter 1987a).

It appears that early growth in more pelagic species may differ. Young *I. oxyrinchus* showed rapid first year growth rates of 49.0 cm/yr and second year rates of 32.0 cm/yr (Pratt and Casey 1983). They found that growth of *I. oxyrinchus*

was more similar to other species of pelagic fish such as the blue shark, dolphin, and tuna.

Age-Weight

While growth in length was fit with the von Bertalanffy growth equation, a logistic equation provided a significant fit to age-weight data. In a similar manner, Parsons (1987) reported that *Sphyrna tiburo* age-weight data were best fit with a logistic equation. Both the von Bertalanffy and logistic growth equation imply that the increase in length and weight of *C. limbatus* is asymptotic. Ricker (1979) cited contrasting opinions on the feasibility of asymptotic growth for fishes, and stated that usually a few older individuals in a fish population may be considerably larger than the asymptote, particularly in terms of weight. *Carcharhinus limbatus* >10 years old probably grow very little in length each year. The results of this study suggest that *C. limbatus* tends toward a W_∞, and appear to grow very little in weight at older ages.

Age and Growth Estimates

The von Bertalanffy growth equation closely described the growth of *C. limbatus*. Estimated size at birth was approximately 53.0 cm which corresponds closely to that of observed data. Maximum theoretical length from the von Bertalanffy growth equation was 195.0 cm for females and 166.5 cm for males, similar to the maximum length of females and males collected during this study, 183.3 and 165.0 cm, respectively. Maximum lengths reported for *C. limbatus* in the Gulf of Mexico were 191.0 and 175.0 cm for females and males, respectively (Clark and von Schmidt 1965); within the 95% confidence intervals predicted for L_∞ (Table 2). Branstetter (1987) estimated L_∞ at 176.0 cm for blacktip sharks captured in the northwestern Gulf of Mexico although his estimates were with sexes combined (34 females, 13 males). Because growth curves differ between males and females, this underestimates L_∞ for females and overestimates L_∞ for males. This may also influence estimated ages of maturity for the sexes; for example, males included in the growth curve would slow the rate at which the curve approaches a particular size and thus result in an older estimated age at maturity for females.

A positive linear relationship between shark length and centrum radius has been established in many shark species. In *I. oxyrinchus* (Pratt and Casey 1983) and *G. cuvieri* (Branstetter et al. 1987), a curvilinear relationship may be more applicable to the data. In either situation, this allows back-calculation of length at time of ring deposition. Back-calculated sizes were smaller at each age class than sizes from observed and predicted data (Table 3, Figs. 6, 7). Ring deposition occurs during the winter months of December–January; however, 83.4% of the blacktips were captured during May–September; thus the increase in size between time of ring deposition and time of capture produced the above disparity. This situation is less evident in older *C. limbatus* with decreased annual growth rates.

Growth rates estimated for adolescent and mature *C. limbatus* were 9–10 and 3–4 cm TL/yr, respectively. These rates were similar to those found by Branstetter (1987a) in the northwestern Gulf of Mexico, although he reported that lengths at age for female and male *C. limbatus* were similar. This study found a significantly larger total length of females at age 7 or greater. Age at maturity for blacktips captured in the Tampa Bay area and in the northwestern Gulf of Mexico were similar for males (4–5 years) but differed among females. Females reach maturity in 6–7 years near Tampa Bay, and 7–8 years in the northwest Gulf of Mexico. Similarity of life history parameters for *C. limbatus* captured in the Tampa Bay area (Killam 1987), in the east central Gulf of Mexico (Springer 1940; Clark and von Schmidt 1965), and in the northern Gulf (Branstetter 1981, 1987a) suggest a continuous population of this species in the Gulf of Mexico.

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Effects of Nonrandomness on Line Transect Estimates of Dolphin School Abundance

Elizabeth F. Edwards and Pierre M. Kleiber

ABSTRACT: Line transect analysis is a census method that has been used to derive estimates of dolphin school abundance from sightings data collected by observers on tuna purse seine vessels. The method is based on the assumption that movements of the sighting platform (tuna vessel) and sighted objects (dolphin schools) are random with respect to each other. In practice, neither schools nor vessels move randomly. Stratification of sightings data has been used to alleviate partially the effects of this nonrandomness, but the effectiveness of this stratification cannot be tested with data from commercial vessels because the movements of the vessels cannot be controlled.

As an alternative, we have used a relatively simple mathematical simulation model to investigate the severity of bias introduced into school abundance estimates by nonrandom movements of schools and vessels, and by the data stratification procedure. Simulations show that nonrandom movements on a scale of a few hundred miles, coupled with the data stratification procedure, can lead to overestimates of dolphin school abundance by as much as a factor of two. These results focus attention on the need to understand patterns of dolphin school distribution in smaller scales of space and time than have been studied previously, and to develop data stratification methods more robust against the effects of small-scale nonrandomness.

The National Marine Fisheries Service (NMFS) monitors mortality of dolphins involved in fishing operations by the United States purse seine fleet for yellowfin tuna, *Thunnus albacares*, in the eastern tropical Pacific Ocean (ETP), to determine whether mortality has exceeded an annual quota implemented by an act of the U.S. Congress. The quota levels depend upon whether dolphin populations are thought to be increasing or decreasing in number, relative to population levels during previous years.

The most effective method currently available for detecting trends in relative abundance is analysis of population abundance estimates collected over a period of 5–15 years. The most effective method currently available for making these abundance estimates is line transect analysis of dolphin school sightings data (Holt 1987; Buckland and Anganuzzi 1988). Two data sources are available for these line transect estimates of abundance: 1) data collected by observers during research surveys (RSOD—Research Survey Observer Data) and 2) data collected by observers during commercial fishing operations (TVOD—Tuna Vessel Observer Data). NMFS has used RSOD because research surveys can be designed specifically to satisfy the assumptions required by line transect analysis (Smith[1]). However, research surveys are very expensive and are becoming more so. This expense causes RSOD to be sparse relative to TVOD and possibly unavailable in the future.

TVOD are a potential solution to these problems, having three significant advantages over RSOD: TVOD are much more abundant, are relatively inexpensive, and are likely to continue being collected as long as fishermen set on and kill dolphins. Observer-days from tuna vessels account for roughly 95% of the annual observer effort in the ETP, while observer-days from research vessels account for only 5%. TVOD are inexpensive relative to RSOD because TVOD are collected by the observers in addition to monitoring dolphin mortality, the latter being the main reason the observer program was initiated. This monitoring program has been in operation for the past 14 years, will continue into the foreseeable future, and monitors about 30% of trips by purse seiners (both U.S. and non-U.S. vessels) each year in the ETP[2]. Ideally, TVOD could be used in place of RSOD to monitor changes in abundance of dolphins.

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[1]Smith, T. D. 1975. Estimates of sizes of two populations of porpoise (*Stenella*) in the eastern tropical Pacific Ocean. Admin. Rep. No. LJ-75-67. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA.

[2]Inter-American Tropical Tuna Commission, Annual Reports 1980–1988. Scripps Institution of Oceanography, La Jolla, CA 92038.

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Reluctance to use TVOD to monitor the relative abundance of dolphins stem from concerns that TVOD 1) seriously violate some of the fundamental assumptions of line transect analysis (Polachek 1983), 2) are subject to serious but unquantified and possibly inconsistent biases, and 3) may be plagued with artifacts arising from the data collection process. Artifacts include, for example, differences between RSOD and TVOD in the sighting frequencies of various dolphin species reported by observers on research vessels compared to tuna vessels (Barlow and Holt[3]), environmental factors affecting sighting ability (e.g., sun glare, sea state, and cloud cover; Holt and Cologne 1987), and shifting areas of concentrated search effort (Buckland and Anganuzzi 1988). However, problems of this type are common to most commercial fisheries data and analyses derived from them. It is important to determine whether, despite these difficulties, useful estimates can be derived from such data sets.

Toward this end, we have developed a relatively simple model simulating the TVOD collection process. Our purpose in developing the model was twofold: 1) to test the effect of suspected biasing factors on line transect estimates of abundance and 2) to test new methods of abundance estimation prior to conducting expensive field tests. There are two unique advantages of simulation modeling in this context. First, we are simulating dolphin abundances and vessel movements within the model itself; therefore, we have available the "truth" against which to compare our model-generated estimates of abundance. Second, we have the capability of investigating effects on estimates that are due to combinations of biasing factors which may not have occurred during the years we happen to have been collecting data, but which can be expected to occur. Biasing factors include, for example, small-scale nonrandomness in school and vessel movements and spatial distributions, choice of data stratification method, changes in fishing objectives, practices, and areas of concentrated search, and changes in sighting protocol and recording procedures. We chose to focus first on the effects of nonrandomness and on the method of data stratification because recently developed methods of line transect analysis to estimate dolphin abundance from TVOD (Buckland and Anganuzzi 1988) raised serious but unanswered questions about the effects of these factors on the abundance estimates derived.

The philosophy behind building a relatively simple model was that biases shown to be troublesome and methods shown to be inadequate in a simple computer model are likely to be even more troublesome and inadequate in the real world. It is both more efficient and more economical to investigate these biases and methods first with a simple simulation model, prior to developing expensive field experiments. We have specifically applied the tenets of Occam's Razor in developing this model, making it as simple as possible while still incorporating the major processes and features contributing to the TVOD data collection process. In this study, we focused only on estimating abundance of dolphin *schools*, leaving questions about abundance of *individual* dolphins for a later day. We also assumed that data were collected without artifacts, leaving also that problem for a later set of simulations. Both of these omissions are examples of factors that probably have strong effects on analyses of TVOD, but which are at this stage unnecessary refinements to the simulation model. Such refinements could be added later if no problems were identified during simulations with the early, most simplified versions of the model.

This paper presents results of testing one hypothesis about one of the most fundamental factors suspected to affect seriously line transect estimates of dolphin abundance derived from TVOD. Specifically, we tested the effect of nonrandom clustering by dolphin schools on abundance estimates. As part of this analysis we tested also the effects of three types of data stratification prior to line transect estimation of school abundance: 1) no stratification, 2) stratification by raw encounter rate per 1° square, and 3) stratification by smoothed encounter rate per 1° square, using the smoothing and interpolation algorithm developed by the Inter-American Tropical Tuna Commission for deriving estimates of dolphin abundance from line transect analysis of TVOD (Buckland and Anganuzzi 1988). We were primarily interested in the third type of stratification, because the properties of the smoothing algorithm are poorly understood. The other two stratifications were conducted to provide a basis for comparison with the smoothing procedure.

[3]Barlow, J., and R. S. Holt. 1986. Geographic distributions of species proportions for dolphins in the eastern tropical Pacific. Admin. Rep. No. LJ-84-27. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA.

THE MODEL

Model Structure

This section presents a general description of model structure. A detailed technical explanation of the model can be found in Kleiber and Edwards[4]. The model (TOPS: Tuna-vessel Observer Program Simulator) simulates the movements of 75 tuna purse seiners and either 2,500 or 1,250 dolphin schools within a 1,200 × 1,200 square nautical mile area. Figure 1 provides a graphical comparison of the "study area" simulated by the model, to the entire area within which the tuna-dolphin association is exploited by the purse seine fleet. Twenty-five hundred dolphin schools is the nominal number of schools expected within a 1,200 × 1,200 nmi area of the ETP, based on Holt's (1985,[5,6] 1987) estimates of the total number of dolphins, average size of dolphin schools, and species proportions for the ETP, prorated from the entire ETP to an area 1,200 × 1,200 nmi. Simulations were also run with half this number of schools to investigate the ability of abundance estimates derived under different conditions to reflect changes in actual abundance in the model. Number of vessels is based on reported size of the ETP purse seine fleet, assuming about 50% of the fleet will be fishing a given area of this size at any one time (see IATTC Annual Reports 1983–87).

All dolphin schools are assumed to be identical (i.e., are replicates); all schools include only the

[4]Kleiber, P. K., and E. F. Edwards. 1988. A model of tuna vessel and dolphin school movement in the eastern tropical Pacific Ocean: technical description of the model. Admin. Rep. No. LJ-88-28. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA.

[5]Holt, R. S. 1985. Estimates of abundance of dolphin stocks taken incidentally in the eastern tropical Pacific yellowfin fishery. Admin. Rep. No. LJ-85-16. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA.

[6]Holt, R. S. 1985. Estimates of population size of dolphins in the eastern tropical Pacific using line transect methods. Admin. Rep. No. LJ-85-20. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA.

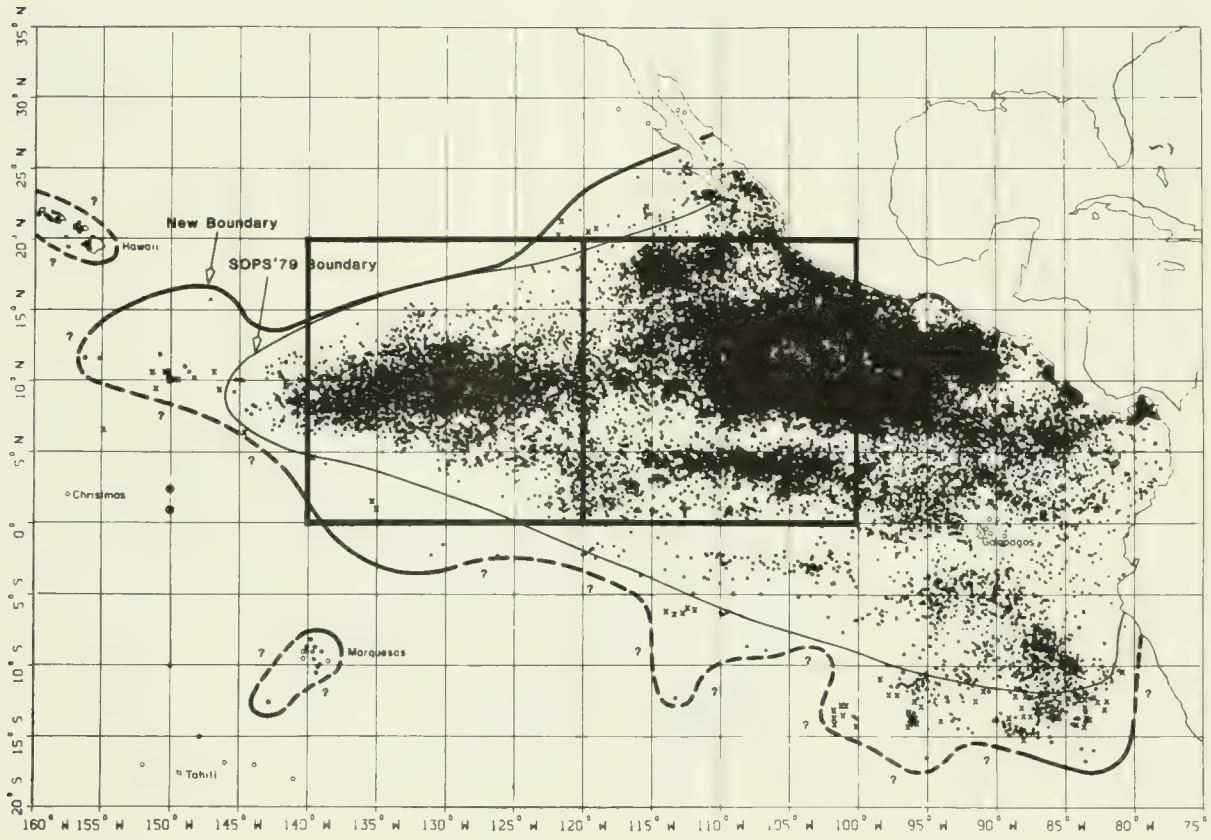


FIGURE 1.—Approximate extent of the eastern tropical Pacific Ocean (ETP) tuna purse seine fishery. Boxes enclose two areas the size of the area simulated by TOPS (1,200 × 1,200 nmi), indicating relative sizes of the entire fishery area compared to the area encompassed by the simulation.

northern offshore stock of spotted dolphins, *Stenella attenuata*, all have the same number of animals, all are equally visible, and all move independently of each other. All vessels are assumed to be identical also; they are the same size, are equally adept at sighting dolphin schools, and do not communicate with each other. Dolphin schools move at speeds varying between 0.5 and 2.4 knots, depending on conditions of the local environment (see below). All vessels move at 15 knots continuously. Speeds are based on reported averages for dolphin schools (Perrin 1979) and for vessels (vessel activity records, NMFS data bases). Vessels are assumed to chase and set upon all sighted schools. Vessels that have set on a school are "removed" from the simulation for 5 hours, simulating the average time to chase, set, collect tuna, release dolphins, and get back under way. Sighted schools are removed from the position of sighting and replaced randomly within 0 to 50 nmi of the sighting, simulating a variable "rest" period of 0 to 24 hours between one set and the next for sighted schools.

Dolphin schools move in response to the local height and gradient of an "environmental topography". The topography is a grid of equally spaced peaks of good habitat interrupted by valleys of low-quality habitat. Habitat quality varies between a value of 1 at the peaks for optimum habitats to 0 at the least favorable habitats midway between peaks. Topographies are generated as a function of sine waves in two-dimensional space and are either stationary or made to slide from right to left at 1 knot. Two combinations of peak spacing and peak shape were used for the simulations reported here: 1) a simple topography of 4 equally spaced peaks with relatively gentle slopes (Fig. 2a), and 2) a more complex topography of 16 equally spaced peaks with relatively steep slopes (Fig. 2b).

These choices for peak number generate spaces between peak tops of 300 and 600 miles. These spacings were chosen based on approximate distances between clusters of dolphin school sightings from research vessel data[7]. Peak steepness was chosen to simulate either slow spatial changes in environmental conditions (gentle slope) or rapidly changing conditions (steep slope) such as those which pertain at ocean fronts (Owen 1981).

Spacings of 600 miles between gently sloping peaks generates distances of 300 miles between maximum and minimum values of the environ-

[7]R. S. Holt, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. July 1987.

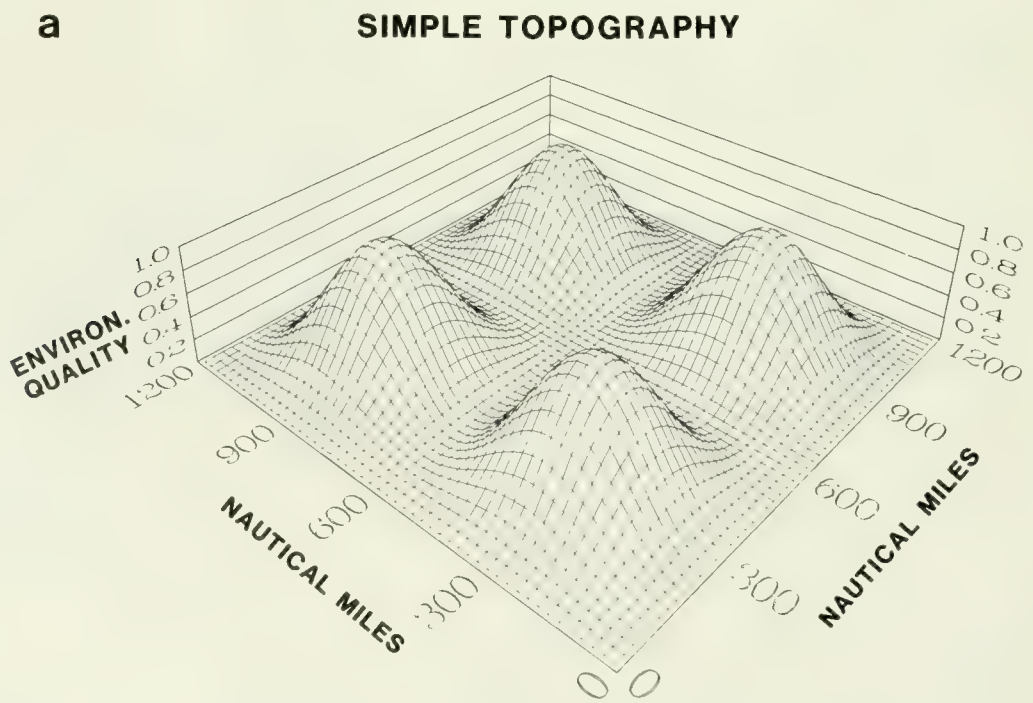


FIGURE 2.—Geometric configuration of the simple environmental

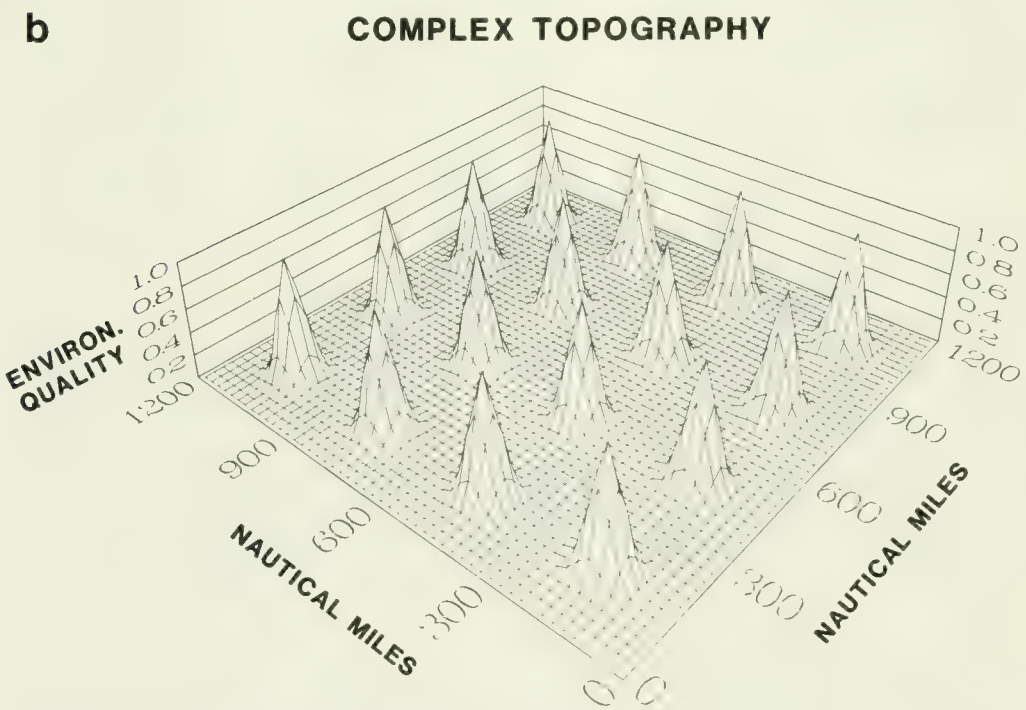
mental topography, representing a 300 mile gradual gradient from "best" to "worst" conditions (Fig. 2a). In the complex, steep environment the precipitous slopes generate a distance of only about 75 miles between maximum and minimum values for environmental quality, the slopes being separated by a "desert" of unfavorable habitat about 150 miles wide (Fig. 2b).

These two topographies were chosen to *bracket* a range of reasonable possibilities for patterns in environmental characteristics that may cause nonrandom clustering of dolphin schools. The factors of peak gradient and peak spacing (number of peaks) are confounded here because we tested only the two topographies, simple:gentle and complex:steep. Gentle gradients are confounded with few peaks; steep gradients are confounded with many peaks. We did not test the other two possibilities (simple:steep and complex:gentle) because these are both intermediate topographies that would have generated intermediate results. In the interest of simplicity, we restrict this simulation study to the two extreme cases.

The rate at which the topography moved (1 knot) was chosen to simulate movement of major habitat features affecting dolphin school movements. Because direct identification and measurements of such features have yet to be made, the choice of rate was based on reported speeds of major ocean currents in the eastern tropical Pacific and apparent seasonal movements of major concentrations of dolphin schools. Reported current speeds include 0.1 to 0.3 knots for the core of the Pacific North Equatorial Current bordering the fishery area on the north (Seckel 1975), 1.2 to 2.4 knots for the equatorial undercurrent underlying the fishery area (Wyrtki 1966), and 1.2 to 2.4 knots for maximum speed of the Equatorial Countercurrent surface waters encompassing a majority of the fishing area (Wyrtki 1966). School sightings data from research ships indicate that major concentrations of dolphin schools may move seasonally between distant areas at approximately 0.3 knots (200 nmi/mo)[8].

Our choice of 1 knot was based on the assumption that the mechanism(s) responsible for aggregating dolphin schools are most probably related to distributions of prey and water mass signatures indicating presence or absence of the prey. Dolphins in the ETP consume small (10–50 cm) fish and squid (Perrin et al. 1973). This mobile prey base will in turn be responding to

[8]S. B. Reilly, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. December 1987.



topography (a) and the complex topography (b).

movements of its own prey base of smaller animals. We reasoned that it is unlikely that this food chain is being swept along as rapidly as the maximum current speeds, but, especially on smaller scales, the distributions of prey and predator are probably moving faster than the speeds apparently characteristic of large-scale seasonal movements. We chose 1 knot as a conservative approximation. It is possible that dolphin aggregating mechanisms move, overall, more slowly than 1 knot, but probably not faster. Thus by comparing simulation results from nonmoving topographies versus topographies moving at 1 knot, we have tried to bracket the range of responses likely to occur in the real system.

In our model, dolphin schools were made to respond to these topographies by adjusting their *speed* according to the quality *level* and by adjusting their *direction* according to the gradient in quality experienced during the previous time step. The range of speeds chosen for dolphin schools (0.5 to 2.4 knots) was based on average observed cruising speeds of dolphin schools in the ETP[9]. In the model, dolphin speed is fastest at the lowest quality levels and slowest at the highest quality levels. Direction choice is stochastic with probabilities biased in the forward direction when the gradient is positive (conditions improving) and in the reverse direction when the gradient is negative (conditions deteriorating). Thus the rules for school speed and direction cause schools to circle slowly in "favorable" areas (i.e., on the peaks) and to move rapidly straight ahead in "unfavorable" areas (i.e., the valleys between peaks).

Vessel movements were controlled by each vessel's history of dolphin school sightings, through a "sightings memory" variable. The value of the variable increases by one unit each time a school is sighted and it decays constantly by a given proportion with each time step. Thus, the value of the variable will be high when a vessel is in a "good" area (i.e., has seen lots of schools) and will be low when the vessel is in a "bad" area (schools are few). Vessel direction is stochastic and affected by the value of this "sightings memory" variable. When the value is high, direction choice is biased in the reverse direction; i.e., the vessel is most likely to turn approximately 180 degrees. When the value is low, small angles are much more likely to be chosen; i.e., the vessel will tend to continue moving forward. Each vessel maintains its own sightings variable independent of the sightings variables of other vessels, so that each vessel moves independently of all other vessels.

Generation of Simulated TVOD

Each simulation began with totally random distributions of both vessels and dolphin schools. Nonrandom spatial distributions of vessels and schools then developed as a function of the environmental topography and of the movement rules for schools and vessels. Each simulation continued for 600 time steps of 1 h/step.

Estimates of school abundance were based only on TVOD collected during the last 200 steps. By this time, the model had in all cases settled into a quasi-steady state (Fig. 3). TVOD for each vessel, collected during each of these last 200 steps, included vessel number, total number of miles searched during that step, position of the vessel at the end of the step, and presence or absence of a school sighting. Only one school could be sighted per vessel per time step.

TVOD were "collected" for all dolphin schools moving within 2 nmi of any vessel. Two nautical miles is the effective strip width found commonly with line transect analyses of real TVOD.[10] All vessels were assumed to carry observers. Observers were always on duty collecting data (i.e., were never "off effort"). Vessels searched continuously (i.e., did not stop at "night").

Data Analyses

TVOD were aggregated subsequently into 1° squares prior to abundance estimation. One-degree squares are the smallest geographic subdivision that retains, with real TVOD, sufficient data for line transect analysis (Polachek 1983; Buckland and Anganuzzi 1988).

Four replicated simulations were conducted for each of eight different cases representing two

[9]Hedgepeth, J. 1985. Database for dolphin tagging operations in the eastern tropical Pacific, 1969–1978, with discussion of 1978 tagging results. Admin. Rep. No. LJ-85-03. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, La Jolla, CA.

[10]M. Hall, Inter-American Tropical Tuna Commission, c/o Scripps Institution of Oceanography, La Jolla, CA 92093, pers. commun.

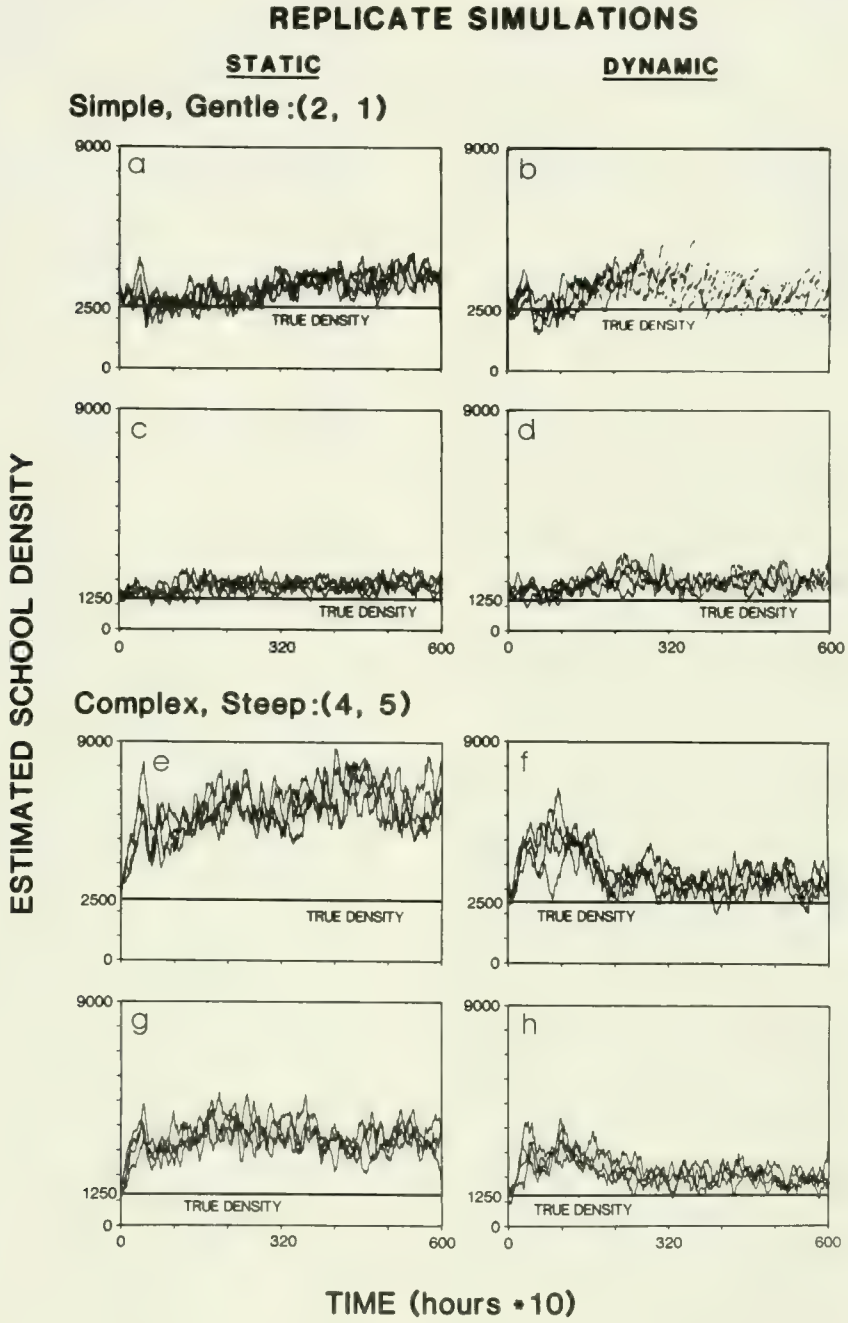


FIGURE 3.—Time course of total school abundance estimates derived from unstratified TVOD. Estimates were derived during each of 600 time steps for 4 replicated runs of 8 different starting conditions. The cases differed in environmental topography (simple, gentle vs. complex, steep), in whether the topography was static or dynamic (sliding left at 1 knot), and in underlying abundance of dolphin schools (1,250 or 2,500). Numbers in parentheses (2, 1; 4, 5) are parameters used in the equations generating the topographies.

levels for each of three factors. The factors and levels included 1) complexity of the environmental topography (simple, with 4 gently sloping peaks vs. complex, with 16 steeply sloping peaks), 2) topography dynamics (static vs. moving at 1 knot) and 3) dolphin school abundance (2,500 vs. 1,250 schools). Topography movement was implemented by causing the grid

of peaks and valleys to slide uniformly sideways from "right" to "left".

Stratification Schemes

TVOD collected under each of the eight cases were subjected to three types of stratification: 1) none, 2) raw encounter rate, and 3) smoothed encounter rate.

In the case of no stratification, school abundance was estimated simply as

$$(TE/AS) * (TA) \quad (1)$$

where TE is total number encounters by all vessels during time steps 400 to 600, AS is total area searched during that time, and TA is total area simulated (1,200 × 1,200 nmi). In this case, all 1° squares were treated as a single group or stratum.

In stratifying by raw encounter rate, encounter rates (schools encountered per nautical miles searched during the last 200 time steps) were calculated for each 1° square. The squares were subsequently ranked in ascending order of encounter rate, and grouped into (n) strata. Strata were demarcated on the basis of including at least (m) schools (encounters) per stratum. Both (n) and (m) were calculated using an algorithm developed by the Inter-American Tropical Tuna Commission for their line transect analyses of dolphin abundance in the ETP (Buckland and Anganuzzi 1988). School abundance was then estimated for each stratum separately. Total school abundance in the entire 1,200 × 1,200 nmi area was then estimated simply as the sum of these estimates per stratum.

In stratifying by smoothed encounter rate, encounter rates in each 1° square were smoothed according to the algorithms developed by Buckland and Anganuzzi (1988). Squares were then ranked and assigned to strata based on these smoothed encounter rates. This smoothing algorithm generally creates strata composed of contiguous areas of squares, arrayed in decreasing order from area of apparent high density to areas of lower density. It is not uncommon, however, for some squares in a given strata to be scattered in areas isolated from the majority for that stratum.

The smoothed encounter rates generated by the algorithm were used only during this stratification step; school abundances were estimated for each stratum using the raw (actual) encounter rate. Total abundance of dolphin schools was then estimated as the sum of the estimates for each stratum.

Estimates Derived

Two types of estimates were derived from these simulated TVOD: *total* abundance of dolphin schools in the entire simulated area, and *change* in school abundance from one sampling period to another, where this change was estimated simply as the ratio of school abundance estimates derived under two different sets of initial conditions in the model. Thus, school abundances were estimated first, and change estimates derived subsequently from these abundances. These estimates of change were calculated as a very simple analogy to a trend estimate, extending in this case over two sampling periods instead of over series of estimates. This two-sample change estimate is only a rough approximation to a trend estimate derived from a series of measurements (Gerodette 1987). However, conclusions about the effects of inconsistent biases on this *change* estimate will be valid for *trend* estimates also, except for the unlikely case in which effects of various inconsistent biases cancel each other out, so that the trend estimate reflects the actual trend, but only fortuitously.

Change estimates were derived under two conditions. Under the first condition the estimate was simply the ratio of the abundance estimate when true density was 1,250 schools (low density) to the estimate when the true density was 2,500 schools (high density). All other conditions in the model remained the same. This simulates the situation of consistent biases.

Under the second condition, the trend estimate was the ratio of one low-density estimate to one high-density estimate, but the ratio was constructed by selecting abundance estimates from cases which differed in other factors in addition to differing in dolphin abundance. This simulates the situation of biases being inconsistent from one sampling period to the next. Three ratios were selected from the many possibilities, to simulate three reasonable scenarios in the real ETP and to bracket a range from mild to severe inconsistencies.

The first of the three ratios was an estimate of abundance change in the simple environment, where in one case the environment was static during the sampling period and in the other the environment was moving at 1 knot. The second

ratio was an estimate of abundance change coupled with a change in the environment from simple to complex (environments remaining static in both cases). The third ratio was an estimate of abundance change coupled with a change from a simple and static environment to a complex and moving environment. These three cases simulated ratio estimates of abundance changes from, for example, one year to the next, where conditions in the environment have also changed between years.

RESULTS

Development of Nonrandom Distributions

Relatively similar dynamics occurred within the four replicated runs of each of the eight cases (Fig. 3). In all cases, nonstratified estimates of total school abundance, calculated for each of the 600 time steps, developed progressively positive biases. Early during each simulation, estimates were relatively accurate. But as schools and vessels became progressively nonrandomly distributed (Fig. 3a–h), estimates deteriorated owing to the concentration of search effort by tuna vessels in the areas where dolphin school were prevalent and to the concomitant avoidance by vessels of areas with few schools.

Although positive bias developed in all cases, the degree and progression of bias was strongly influenced by environmental topography, both configuration and dynamics. Relatively little bias developed in cases where the topography was relatively noncomplex (Fig. 3a, c) or was moving at 1 knot (Fig. 3b, d, f, h). Very large biases developed in cases where the topography was complex and static (Fig. 3e, g).

School Abundance Estimates

Nonstratified estimates of total school abundance, calculated from TVOD collected during the last 200 time steps, show the positive bias indicated in the time courses shown in Figure 3. The degree of positive bias in unstratified estimates was not constant, but varied with model conditions (Fig. 4). Bias was least for the case of a simple, moving environment, slightly higher for the complex, moving environment, slightly higher again for the simple, static environment, and dramatically higher for the complex, static environment.

Estimates of school abundance based on stratification by raw encounter rate were in all cases relatively accurate, although estimates tended to be negatively biased for the cases of a simple environment (Fig. 4).

Estimates based on stratification by smoothed encounter rate also tended to be negatively biased for the cases of a simple environment (Fig. 4). The case of a complex, moving environment led to a slight positive bias in abundance estimates. But the complex, static environment led to pronounced overestimates of abundance that rivaled results from the unstratified analyses.

Reducing the underlying density of schools by half, from 2,500 to 1,250 schools, was mirrored by decreases of approximately one half in school abundance estimates (Fig. 4). Patterns of over- or underestimation under various model conditions remained consistent over both densitites. For example, the most severe bias occurred in both cases under conditions of a complex, static environmental topography.

Change Estimates

When change estimates were derived by comparing cases in which only the underlying density of schools was changed (i.e., when biases remained consistent between sampling periods) the estimates based on raw or smoothed encounter rate stratification were very accurate (Fig. 5). Estimates based on unstratified data were strongly biased but analyses of real TVOD are never conducted on unstratified data, so this case is useful only as an indication of improvement in estimation achieved by stratifying.

Inconsistent biases produced a dramatically different result. Even relatively small changes in underlying model conditions produced moderate to large biases in the change estimates. Also, these biases were neither consistently positive nor consistently negative, even within a single set of comparisons (Fig. 5).

DISCUSSION

School Abundance Estimates

Stratification

Overestimates were derived from nonstratified data in all cases because vessels (and therefore observers) spent more time (expended more effort) in areas where dolphin schools were abun-

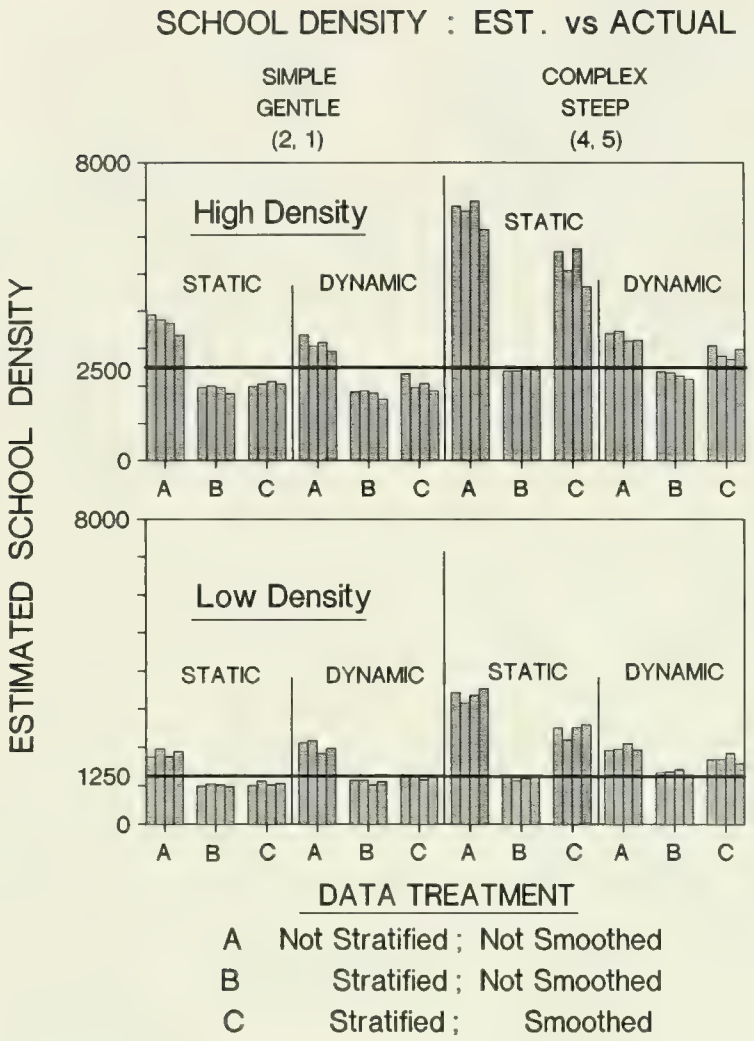


FIGURE 4.—Estimated vs. actual school density (total number of schools in simulated area) under 8 different cases for model conditions and under 3 types of data simulation for each condition. Each set of 4 columns is a set of 4 replicated runs for a given case. The cases differed in 1) environmental topography (simple, gentle vs. complex, steep), 2) whether the topography was static or dynamic (sliding left at 1 knot), and 3) actual abundance of dolphin schools (1,250 or 2,500). Numbers in parentheses (2, 1; 4, 5) are parameters used in equations generating the topographies. Two and 4 refer to the number of peaks arrayed along each axis of the spatial plane, generating a regular square grid of peaks. One and 5 are values of the parameter controlling peak slope; 1 generates a gradual slope, 5 generates a precipitous slope. Heavy lines across the figures indicate the true density (abundance) of schools in each set of simulations. Data treatments include A) no stratification before estimating school abundance, B) stratification of 1° squares based on observed (raw) encounter rates per square, and C) stratification of 1° squares based on smoothed encounter rates per square.

dant, and avoided areas where schools were few (Fig. 6). Overestimates of average school abundance per 1° square resulted from this pattern of effort because few samples from low density squares contributed to the average. Overestimates of total school abundance then followed directly by extrapolating this overestimate to the entire area.

Overestimation of school abundance was especially pronounced for the case of a complex,

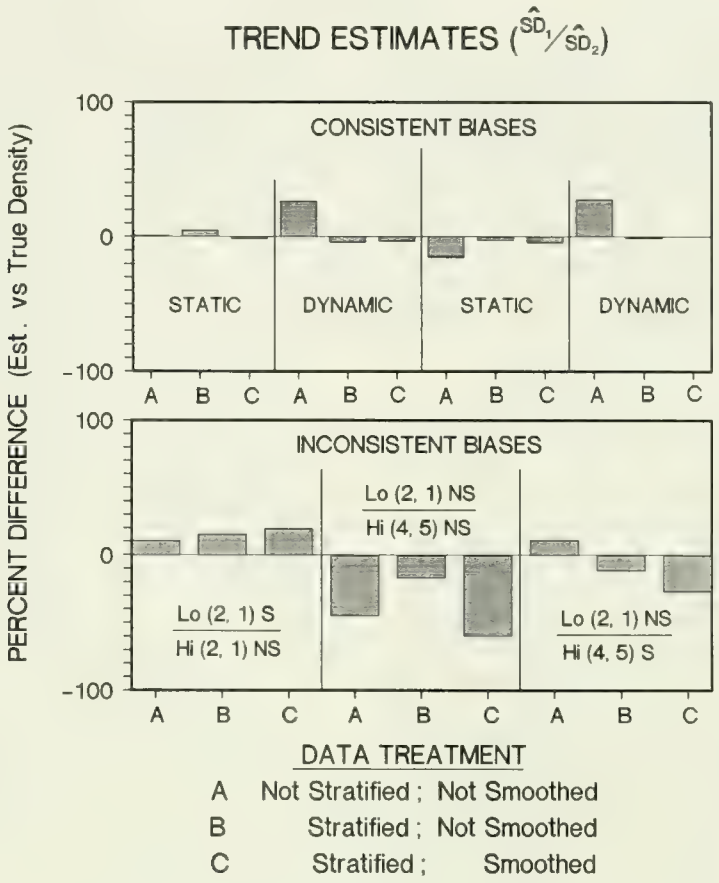


FIGURE 5.—Comparisons of estimated versus actual change ("trend") in school abundance from one sampling period to another. Changes in abundance were estimated as the ratio of school abundance (estimated or actual) under one set of model conditions (SD_1) to school abundance (estimated or actual) under some other set of conditions (SD_2). Lo and Hi refer to actual abundance of schools (Lo = 1,250 schools, Hi = 2,500 schools). S and NS refer to topography dynamics (S = topography sliding sideways at 1 knot (dynamic), NS = static topography). Number in parentheses refer to parameters generating topographies. Two and 4 refer to number of peaks along each axis. One and 5 refer to peak gradient (1 = gradual slope, 5 = precipitous slope). Three change estimates, resulting from three different types of data stratification, were generated for each comparison: A) no stratification before estimating school abundance, B) stratification of 1° squares based on observed (raw) encounter rates per square, and C) stratification of 1° squares based on smoothed encounter rates per square. Comparisons are expressed as (1 – (Estimated change/actual change))*100, so that differences appear as percentages. Differences are 0 when estimated changes equal actual changes.

static environment because this condition led to very concentrated clumping of schools within a few 1° squares. Vessels concentrated most of their effort in these few squares with very high density. Overestimates were less pronounced in the cases of a simple environment because here the areas of higher density were much more diffused and not so different from areas of low density. The gradient of increasing density toward the topographic peaks built up much more slowly, so that vessels sampled many more squares with relatively low density than had been the case for the complex, static environment. The overestimate of abundance was relatively lower for the case of the complex, dynamic environment for essentially the same reason; the

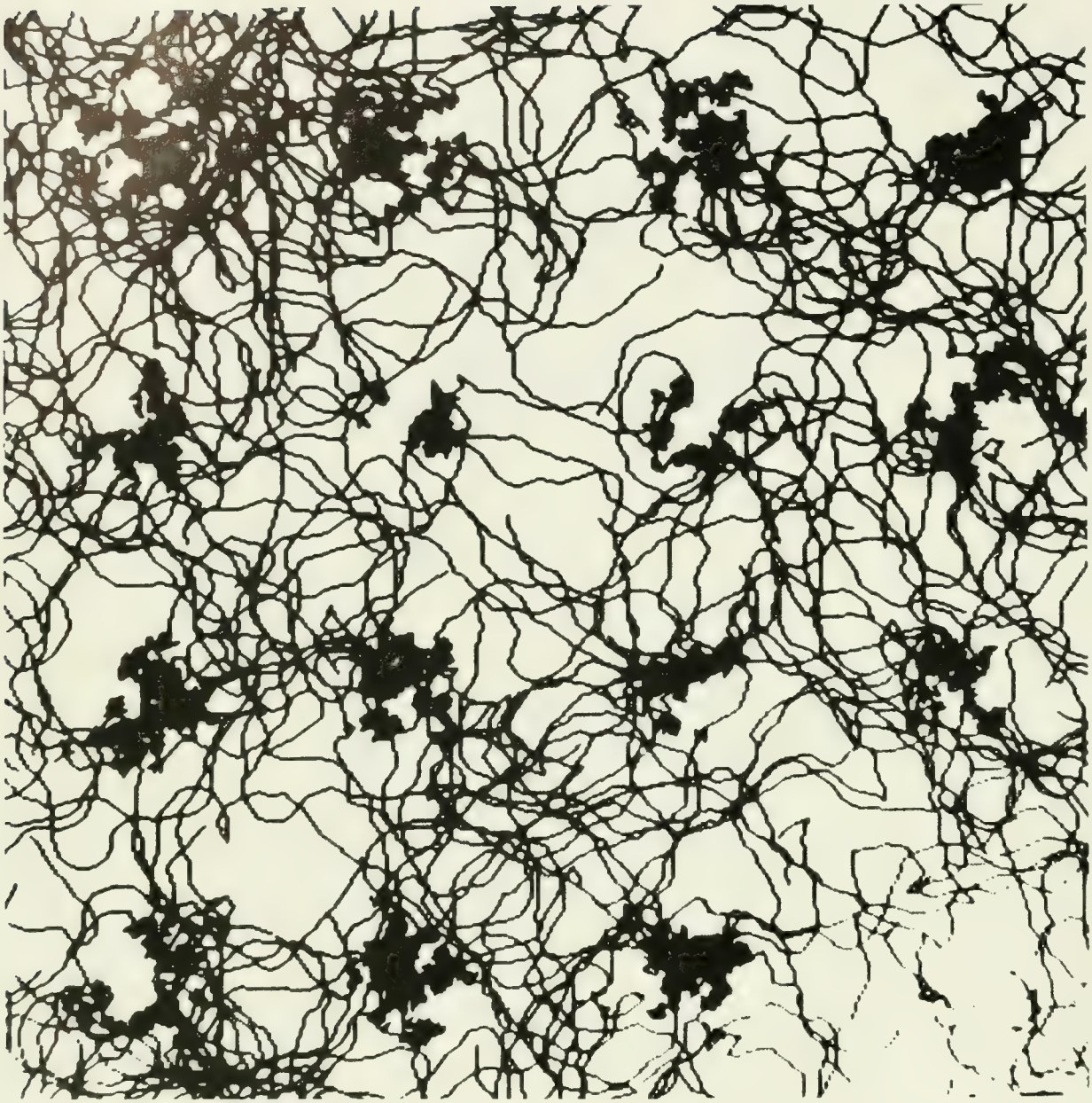


FIGURE 6.—Tracks of simulated purse seine vessels after 400 time steps during a simulation with a complex, static environmental topography. Vessel movements are concentrated near peaks in the topography, in response to the high density of dolphin schools in these areas.

characteristics of the environment produced many more squares with relatively low densitites. But here the process generating these relatively low-density squares was very different from the simple environment case. In the complex, moving environment the peaks were moving at 1 knot. Aggregating the data from the last 200 time steps generated a smeared version of the underlying 16-peak array. Integrated over the entire period of data collection, the areas of dolphin concentration appear as bands across the simulated area, rather than as individual peaks (Fig. 7). The dolphin schools spread themselves out over a larger number of squares than in the static case, producing lower estimates of average density per square.

Stratification By Raw Encounter Rate

Estimates derived from stratification by raw encounter rate were relatively unbiased in all cases because in these simulations we "collected"

an unrealistically large number of TVOD with unrealistically complete coverage of the simulated area. Of the four hundred 1° squares in our 1,200 × 1,200 nmi area, no more than six went unsampled during any simulation. As a result, encounter rates in each square reflected very accurately the true school density in each square. Stratifying by these encounter rates, deriving a different estimate of average school density for each stratum, taking the weighted average of these estimates, and then extrapolating this weighted average to the entire area produced quite accurate estimates of total school abundance.

The slight negative bias in the cases of a simple environment may be due to a curious effect that was not obvious until we made a movie of vessel and school movements generated by TOPS for a simulation of the simple moving topography. It appears in this movie that vessels tend to undersample the areas of highest density in the center of the gradual peaks, because the vessels encounter enough schools along the periphery to keep them from turning into these high density, central areas. Undersampling the highest densities of course will lead to an underestimate of the average density per square and thus to an underestimate of total abundance.

This avoidance of peak centers did not occur with the complex, static environment used in our simulations, apparently because most of the peak area in this topography occurred within only a few squares (Fig. 2b). Vessel speed was apparently sufficient to carry most vessels into the highest density areas before the effects of sightings caused the vessels to slow down.

Stratification by Smoothed and Interpolated Encounter Rate

Given the apparent accuracy of estimates derived under the stratification by raw encounter rate, it would seem irrelevant to proceed to the more complicated and sometimes ineffective stratification by smoothed encounter rates. However, real world tuna vessels never sample the ETP as completely as the simulated vessels sampled the TOPS environments. In most years, fewer than half the vessels carry observers, the fleet as a whole samples less than half the entire ETP, and the sampling that is done tends to be concentrated seasonally in variable geographic areas (Buckland and Anganuzzi 1988). This leaves many 1° squares unsampled.

For management purposes, we cannot assume that squares with no effort contained no dolphins; therefore, we are left with the necessity of estimating densities in those unsampled areas. We have to fill in the holes somehow, so an interpolation method, either a more robust method than used to date, or some new method, is required.

In most of the TOPS simulations, Buckland and Anganuzzi's (1988) smoothing and interpolation routines worked quite well, with accuracy rivaling that of the raw encounter rate stratification. The very poor performance of the smoothing algorithm in the case of a complex, static environment, however, is troubling because we have no data from the field to determine whether or not such topographies exist in the ETP. We suspect that such topographies do exist because the parameters used in the TOPS model were chosen specifically to be reasonable. In particular, the distances between peaks were chosen to bracket the apparent distances between clusters of dolphin schools as indicated by sightings from research vessels.[11] Also, the movement rates by vessels, schools, and topography were specifically selected to approximate observed rates.

The severe bias in the complex static case arises owing to an interaction between the effective sampling frequency (in this case, 1° squares), the peak topography, and the mechanics of the smoothing algorithm. The algorithm works by calculating, for each square, a smoothed encounter rate that is a weighted average of encounter rates for all squares within a radius of at least four squares. Thus the smoothed rate in each square is affected by rates across a diameter of at least eight 1° squares, or a distance of at least 480 nmi (8 × 60 nmi). In the case of the complex, static topography, this minimum distance is greater than the distance between peaks (300 nmi). Also, the relatively precipitous peaks encompass only 3 or 4 squares and are separated by low-density areas several squares across. The smoothing algorithm tends to "fill in" these low-density areas, elevating apparent encounter rates in the intervening squares and causing squares to be assigned to strata out of proportion to the true densities of dolphin schools in the squares.

It is possible that the relatively precipitous slopes of the peaks in the complex environment

[11]R. S. Holt, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun. December 1987.

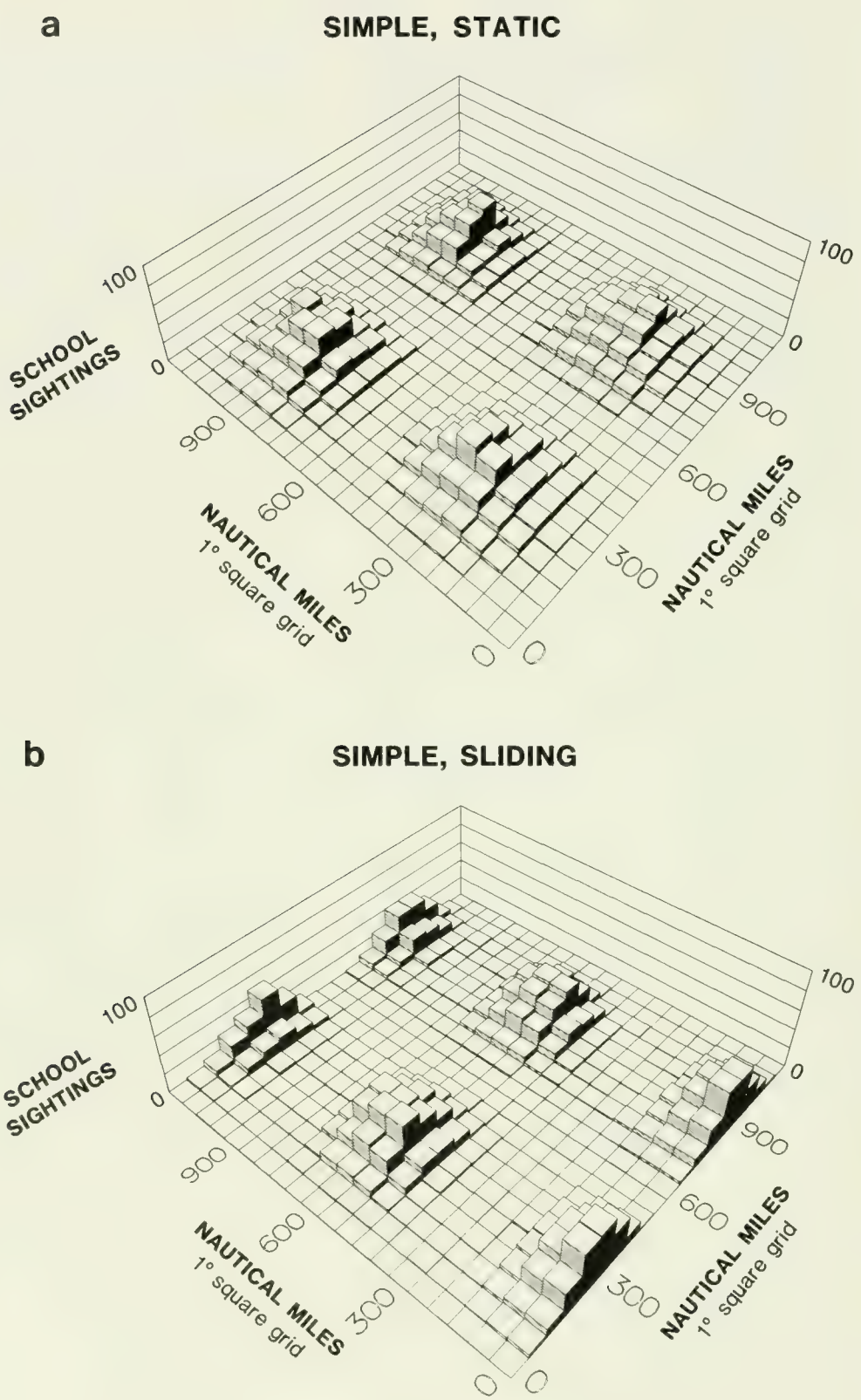
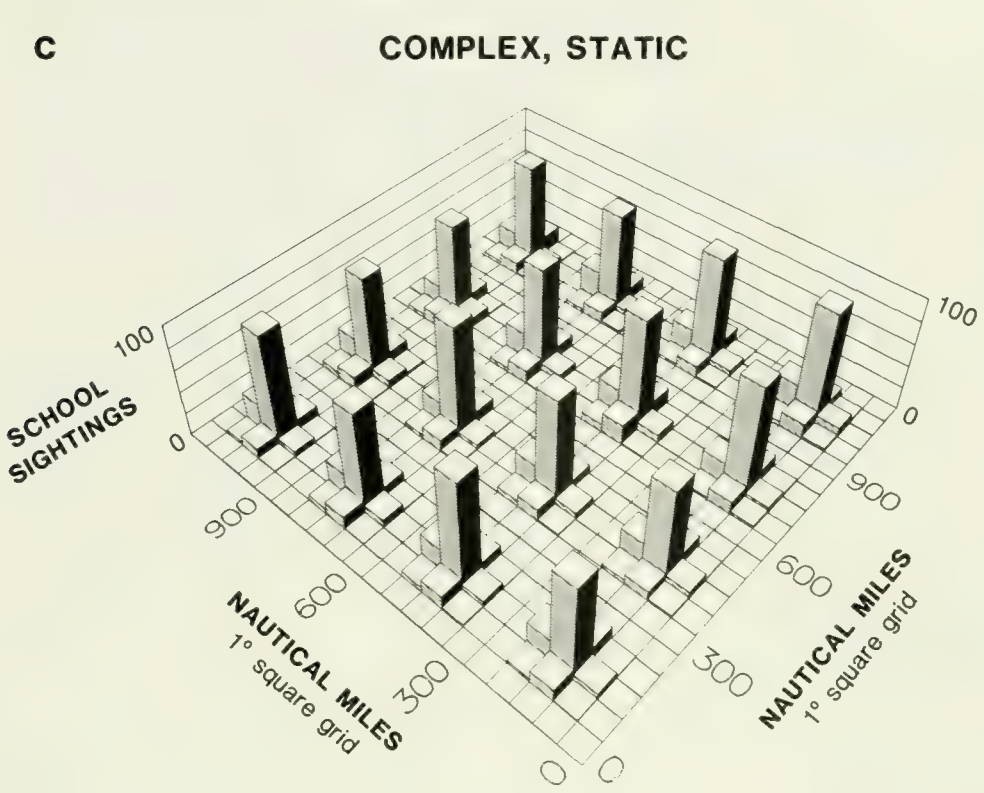
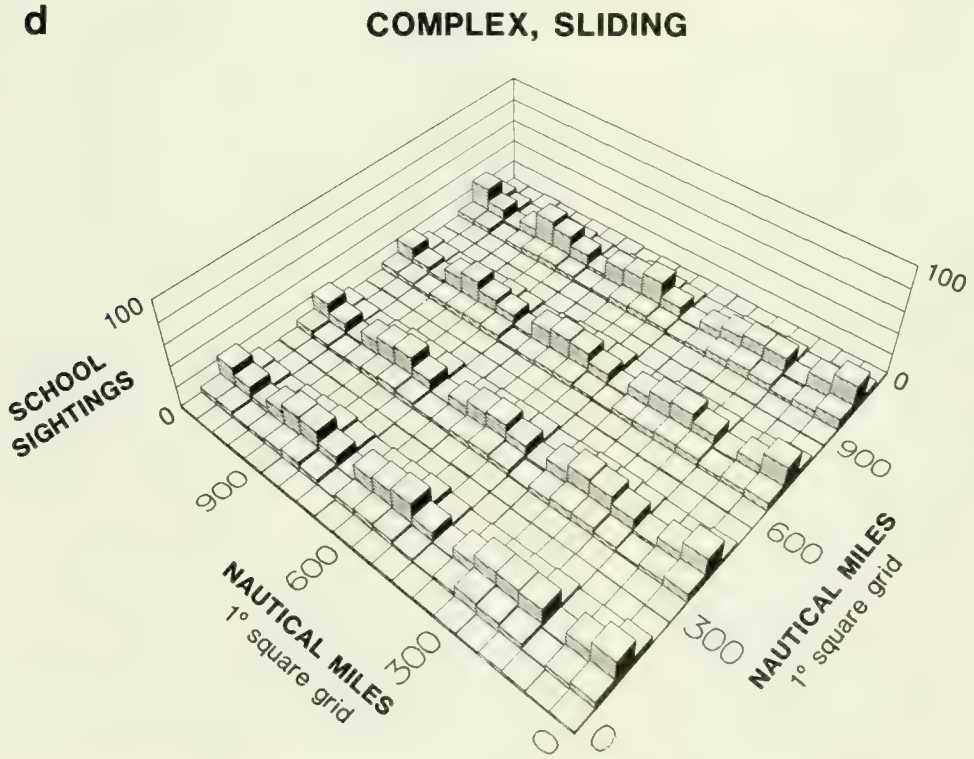


FIGURE 7.—Average number of sightings of dolphin schools per 1° square during the last 200
a) simple, static, b) simple, sliding,





time steps of one simulation for each of the four types of environmental topography
c) complex, static, and d) complex, sliding.

are unrealistic, but in fact these slopes extend over at least two 1° squares (Fig. 2b). This is a distance of at least 120 nmi. Conditions change across ocean fronts in distances much shorter than this, and ocean fronts are aggregating mechanisms for many marine biota (Owen 1981). Of course, such fronts are never static and the smoothing algorithm worked quite well in the complex, dynamic environment, apparently owing to the smearing effect discussed previously. However, as in the previous case, we have as yet insufficient data to identify the conditions actually pertaining in the real ETP.

The major point is that the simulations have shown that clustering characteristics on relatively small scales (10s to 100s of miles) can seriously bias estimates of abundance derived via the smoothing algorithm, which is a problem because as yet we know almost nothing about clustering on this scale in the real ETP. The model results indicate strongly that future research should be focused either on resolving this lack of information or on developing alternative analyses that are not as sensitive as this smoothing algorithm to these small-scale spatial effects.

Change Estimates

These demonstrated problems with estimating school abundance are serious but in real-world analyses could perhaps be ignored; the next set of dolphin quotas will be determined not on the basis of estimated absolute abundance at some point in time but rather on the basis of *estimated changes* in abundance (Holt et al. 1987). This is an advantage in the estimation process because as long as nothing other than dolphin abundance changes from one sampling period to the next (i.e., as long as biases remain consistent), then accurate estimates of those changes in abundance can be derived from TVOD.

However, we know almost as little about whether biases truly remain constant (consistent) in the ETP, as we know about small-scale spatial distributions of dolphin schools. It is obvious from Figure 5 that even relatively small changes in bias can lead to considerably inaccurate estimates of change and, by implication, estimates of trend. A change as simple as moving from a static to a slowly moving environment produced an overestimate in the ratio estimate of almost 20% (Fig. 5, Lo(2, 1)S/Hi(2, 1)NS). Not even the direction of bias remained consistent, changing from positive in some cases to negative in others.

The ratio estimate based on a simple static environment during one sampling and a complex static environment during the other period (Fig. 5) is of particular interest, because an effect of this type may be the basis for the anomalous and biologically unlikely dip in Buckland and Anganuzzi's (1988) estimates of abundance for northern offshore spotted dolphin, *Stenella attenuata* during 1983 (Fig. 8), the year of an exceptionally strong El Niño. Our simulation results in this case lead to a potentially testable hypothesis about a factor that may have significantly affected analyses of real TVOD. Preliminary analyses of apparent differences in distributions of dolphins during El Niño versus non-El Niño years support the hypothesis that changes in spatial distributions led to inconsistent biases and thus to inaccurate trend estimates during these years.[12]

SUMMARY

The results from these simulations are useful in a general sense; they show that significant biases can develop within the simple model structure used here. The quantitative results are specific to the parameter values and movement rules chosen for these particular simulations and are neither intended nor assumed to mirror specific distributions of either vessels or dolphin schools in the real environment of the ETP. Although parameter values controlling rates and abundances are "correct" to the best of our knowledge, choosing different parameters for the functions controlling dolphin responses to the environment, or vessel responses to dolphins, would probably change both the rates and spatial characteristics of pattern development and thus estimates of abundance derived.

Other clustering patterns could have been used, and other results generated. However, our purpose at this stage was not to generate a catalogue of patterns and responses. Our purpose was to test the effects of varying a simple but reasonably realistic (in terms of rates and spacings) aggregating pattern for dolphin schools, using the results to determine whether any insight could be gained into the problem of estimating abundance of dolphin schools in the real world, using real TVOD.

Indeed, we found that our simplified simula-

[12]S. B. Reilly, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038, pers. commun.

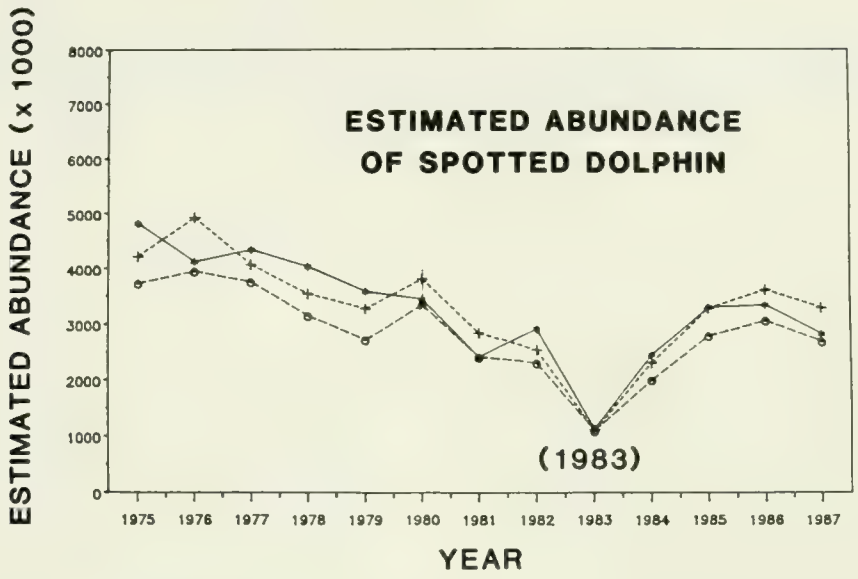


FIGURE 8.—Estimated abundance of northern offshore spotted dolphin, *Stenella attenuata*, showing biologically unlikely recovery in 1984 following apparent decrease in abundance during 1983 (from Buckland and Anganuzzi 1988).

tion approach identified two critical problems that must be addressed if TVOD are to an effective source for estimates of dolphin abundance or changes in abundance in the eastern tropical Pacific Ocean. These critical problems are 1) the effect of small-scale nonrandomness of dolphin schools, and 2) the interactions between these small-scale patterns (sampling frequency and smoothing algorithms) on estimates of school abundance or change in abundance derived from line transect analysis of sightings data. Research effort should now be directed toward identifying and characterizing school distributions within these smaller spatial (and temporal) scales, and toward improving the efficacy of existing methods or developing new methods for analyzing TVOD.

ACKNOWLEDGMENTS

Development of the model and preparation of this paper have been aided significantly by the sage advice and helpful criticisms of Steve Reilly and Doug DeMaster.

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Maturation and Reproduction in Two Hawaiian Eteline Snappers, Uku, *Aprion virescens*, and Onaga, *Etelis coruscans*

Alan R. Everson, Happy A. Williams, and Bernard M. Ito

ABSTRACT: Size at sexual maturity, spawning season, and pattern of egg release were determined for two of Hawaii's commercially important snapper species: uku, *Aprion virescens*, and onaga, *Etelis coruscans*. Sexual maturity of females was assessed by macroscopic and microscopic (oocyte measurement and histology) techniques and gonosomatic indexes. Interspecific differences were noted in many aspects of the reproductive biology. Both species had protracted spawning seasons: uku spawned in May-October while onaga spawned in June–November. Female size at sexual maturity was 425–475 mm fork length (FL) for uku and 675–725 mm FL for onaga. Both species were determined to be multiple spawners, although the number of batches spawned per season could not be established.

Uku, *Aprion virescens*, and onaga, *Etelis coruscans* (Lutjanidae), are species of considerable importance in terms of total landings and value to bottom fish fisheries in southern Japan (Masuda et al. 1975), Guam, the Northern Marianas (Amesbury and Myers 1982), Vanuatu (Brouard and Grandperrin 1985), American Samoa (Western Pacific Regional Fishery Management Council (Council) 1986), and Hawaii (Ralston and Kawamoto[1]). In addition, many other Pacific island nations have subsistence and commercial fisheries for these species. In Hawaii, uku and onaga ranked second and third, after *Pristipomoides filamentosus*, in total catch and value among bottom fish species in 1984 (Pooley 1987).

Both species are widely distributed throughout the tropical Indo-Pacific. Uku range from East Africa to Hawaii and from southern Japan to Australia (Allen 1985), and onaga extend to the Atlantic coasts of South America and Africa (Druzhinin 1970). Uku are caught at the surface by trolling gear and at ≤ 300 m depths by deep-sea handline gear (Druzhinin 1970), whereas onaga are restricted to deeper waters between 220 and 320 m. In Hawaii, the greatest portion of the uku and onaga catches comes from the Penguin Bank region, which is southwest of Molokai in the main Hawaiian Islands (Ralston[2]).

Relatively few reproductive studies have been completed for the commercially important bottom fishes of the western Pacific, even though such information represents a critical component of the biological basis of management for the bottom fish and seamount groundfish fisheries in this region (Council 1986). Some information is available on Hawaiian stocks of *P. filamentosus* (Ralston 1981; Kikkawa 1984), *Etelis carbunculus* (Everson 1984), and *Seriola dumerili* (Kikkawa and Everson 1984), but none is available for uku and onaga. Thus, a study was undertaken to determine the size at sexual maturity, spawning season, and pattern of egg release of uku and onaga. Size at sexual maturity is a particularly important parameter used to assess and evaluate the impact of fishing mortality on spawning stock biomass and to determine levels of optimum fishery yield (Polovina 1987). During this study, we also attempted, within the constraints imposed by our sampling program, to develop an efficient method for determining gonad maturity. A third goal was to discern interspecific differences between the reproductive biology of the two species and to interpret those differences.

[1]Ralston, S., and K. E. Kawamoto. 1987. An assessment and description of the status of bottom fish stocks in Hawaii. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396. Southwest Fish. Cent. Admin. Rep. H-87-7, 55 p.

[2]Ralston, S. 1979. A description of the bottomfish fisheries of Hawaii, American Samoa, Guam, and the Northern Marianas. A report submitted to the Western Pacific Regional Fishery Management Council, Honolulu, 102 p. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu HI 96822–2396.

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MATERIALS AND METHODS

Uku and onaga caught in 1984–86 and 1985–87, respectively, by commercial fishermen using deep-sea hook-and-line gear were weighed and measured for fork length (FL), and their capture locations were noted. Most were caught in the main Hawaiian Islands and were sold through the Honolulu wholesale fish auction. Following sale of the fish, viscera were extracted by the purchasing agent and refrigerated with an identifying tag. Gonad samples were collected later and preserved at the laboratory either in modified Gilson's fluid (Bagenal and Braum 1968) or Bouin's fluid.

Sexual maturity of females was evaluated by several methods. First, ovaries were staged macroscopically and given a preliminary maturity stage designation (Hilge 1977) (Table 1). To refine and confirm these macroscopic designations, at least one of the following three additional microscopic techniques was used: volumetric or cork borer subsampling, which is based upon the size and appearance of individual oocytes, or standard histological examination. Hilge's (1977) table was also used to assign a final stage designation to these ovaries. To avoid confusion, prespawning adults prior to vitellogenesis were classified as stage I immature, and prereproductive individuals as stage I juvenile.

To determine oocyte size-frequency distributions by volumetric subsampling, uku ovaries preserved in modified Gilson's fluid were examined. After adequate time for dissolution, connective tissues were removed, and the remaining "free" ova were placed in a flask, which was then filled with 200 mL of water. A homogeneous distribution of ova was obtained by using a magnetic stirrer (Van Dalsen 1977). A 3 mL sample was then pipetted onto a gridded petri dish and examined under a binocular dissecting scope at 50×. With an ocular micrometer, 100–200 oocytes were measured along their longest dimension. This method precluded the need to measure oocytes from various sites within the ovary to determine spatial homogeneity of development. Maturity stages were assigned based upon the largest oocyte mode and the degree of oocyte transparency (Table 1).

Subsamples of ovaries of both species preserved in Bouin's fluid were taken from the anterior portion with a cork borer and examined under a binocular dissecting microscope at 50×. The average diameter of the largest oocyte mode was determined, and the percentage of each maturity stage present was noted. Oocyte diameter frequency plots were constructed for uku ovaries in various stages of development and compared with similar plots constructed by using oocyte diameter data obtained by the volumetric method.

For histological examination, some ovaries of both species representing various visually identifiable maturity stages were transferred from Bouin's fluid to 70% ethanol. Portions of ovaries from 28 uku and 22 onaga caught at various times of the year were embedded in paraffin, sectioned at 5 μm, stained with hematoxylin, and counterstained with eosin. Each was as-

TABLE 1.—Ovary developmental stage designations used for study of the reproductive cycle of uku and onaga. Designations are adapted from Hilge (1977).

Class	Stage	Oocyte developmental status	Gonad external appearance	Stage classification criterion
I	Immature	Oogenesis from oogonium to primary oocyte with cytoplasmic vacuoles beginning to appear	Genit ridge to definite gonad; individual eggs not discernible	Oogonia transparent; primary ooctes translucent
II	Developing	Vitellogenesis	Elongation of the ovary	Opaque yolked oocytes
III	Ripe	Hydration	Swollen; ovary wall thin	Transparent, ripe ova
IV	Spent	Atresia, general cell breakdown	Slack; shrinking ovary; ovary wall thick	Residual ova

signed a maturity stage based on the criteria in Table 1. Oocytes were histologically identified using information provided in Crossland (1977). Sectioned ovaries also were examined for the presence of postovulatory follicles and oocyte atresia, features used to establish criteria for the estimation of spawning frequency and to separate juveniles from prespawning adults for determination of size at sexual maturity (Hunter and Macewicz 1985).

The results of these four visual methods were compared with gonosomatic index (GSI) values [(gonad weight/body weight) × 100]. Gonosomatic indexes were calculated for both species to provide a rapid but preliminary indication of developmental stage, although an insufficient number of uku testes were obtained. Excluded from this analysis were individuals that had not yet reached size at sexual maturity. Spearman's coefficient of rank correlation (Snedecor and Cochran 1978) was used to ascertain whether a positive relationship existed between GSI and maturity stage during the spawning periods for females of each species.

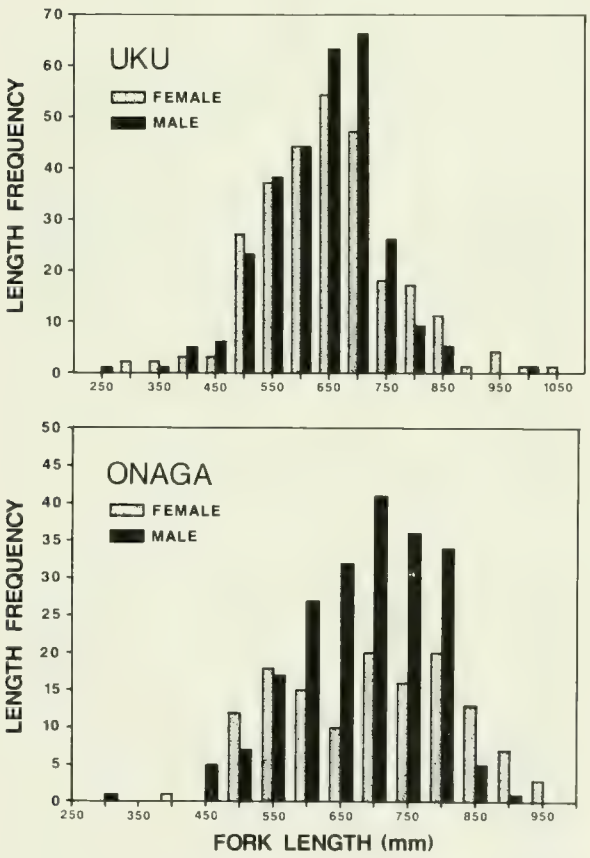


FIGURE 1.—Length-frequency distribution of male and female uku and onaga.

Size at sexual maturity (L_{50}) was defined as the smallest length category in which at least 50% of the individuals were mature (i.e., stage II or beyond, GSI > 1.5) during the spawning season. The logistic equation was fitted to the percentage of mature individuals in each size class (P_x) and FL (Gunderson et al. 1980; Ni and Sandeman 1984); that is

$$P_x = \frac{100}{1 + \exp(a\mathrm{FL} + b)},$$

where a and b are fitted parameters and $L_{50} = -b/a$. We also calculated the percentage of maximum length (MAXLEN) at which sexual maturity occurred. This ratio has been used to compare proportionate size at maturity for species by habitat type, zoographic province, or depth range (Grimes 1987).

Sex ratios were compiled and examined for significant deviation from unity and to determine whether sex ratio and size (in 50 mm FL intervals) were independent using chi-square statistics. Two-way contingency table analysis was performed to determine whether the sex ratio differed during the year when pooled into bimonthly periods.

RESULTS

Spawning Season

Spawning season was determined from a wide size range of uku and onaga (Fig. 1). The Spearman rank correlation coefficients (r_s) calculated by comparing GSI with stages I–III were $r_s = 0.6205$ for uku ($P < 0.0001$), and $r_s = 0.8685$ for onaga ($P < 0.0001$), indicating a positive relationship between GSI and stage of development for both species, although the correlation was considerably lower for uku. In addition, the range in GSI values representing stages II and III ovaries was greater for uku than for onaga (Fig. 2). Thus, rather than using GSI as the single method for estimating spawning seasonality by month or fish length, visual staging methods also were used.

Both species reached maturity in the spring and summer and spawned continuously until fall or early winter. Neither species reached stage II of development (vitellogenesis) at any other time of the year. Uku spawning began in May and peaked 1 month later in June, as evidenced by the sharp rise in GSI values and the presence of mature and ripe fish during this time (Figs. 3, 4).

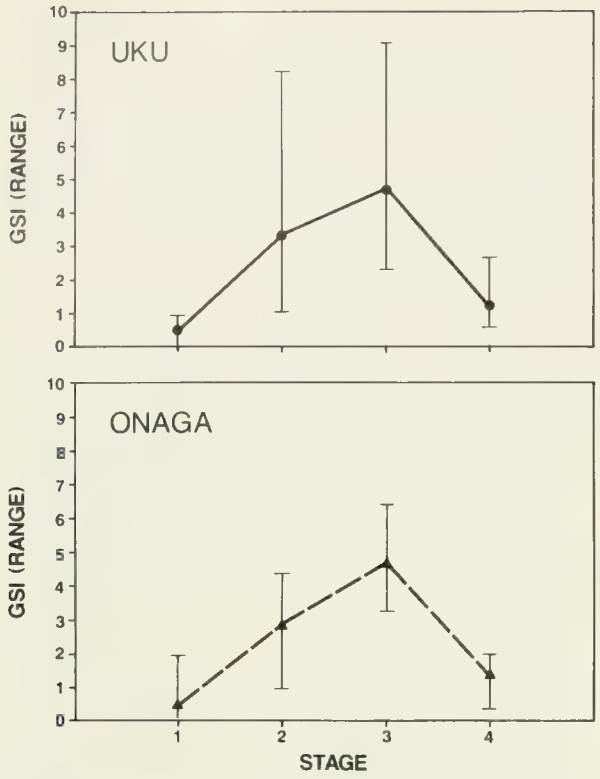


FIGURE 2.—Range in (A) uku and (B) onaga gonosomatic index (GSI) for each developmental stage designation in Table 1.

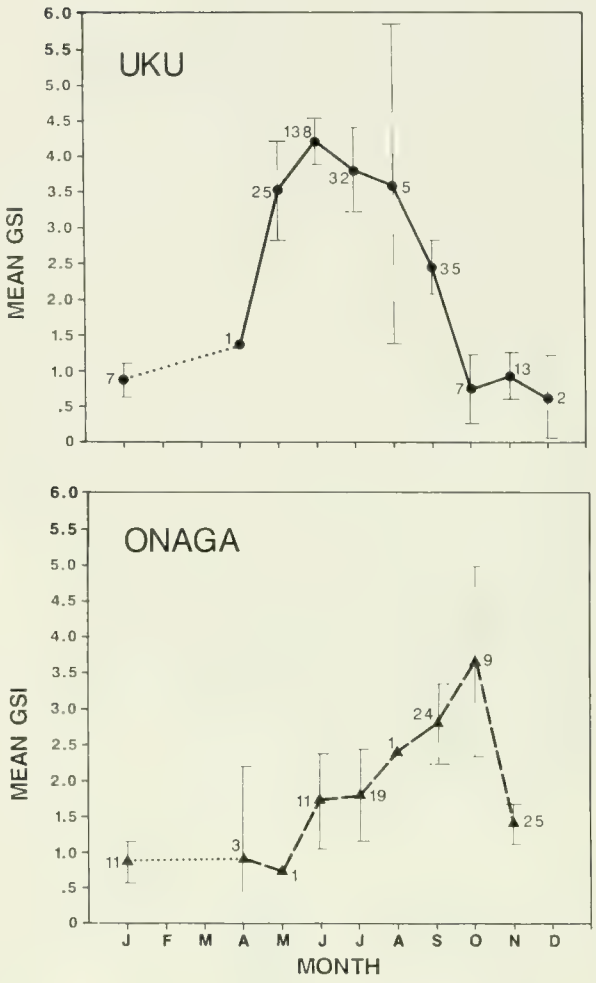


FIGURE 3.—Monthly mean gonosomatic index (GSI) for female uku and onaga. Bars indicate 95% confidence limits. Juvenile (<500 mm FL) uku and juvenile (<600 mm FL) onaga were excluded from analysis. Sample size is indicated next to each data point.

From July to October, the mean GSI values gradually decreased as spawning activity tapered off. By November, all fish examined were either partially or completely spawned (stage IV). Stage IV fish were not found during the spawning season.

In contrast, female onaga began maturing in June. Fully ripe onaga were not found until July, and spawning activity did not peak until October (Figs. 3, 4). The GSI values dropped sharply in November as the incidence of completely spawned and partially spawned individuals abruptly increased. As with uku, completely spawned individuals were not found until the close of the spawning season. Mean monthly GSI values for male onaga reflected a similar pattern.

Size at Sexual Maturity

Uku matured at a substantially smaller size than onaga. Fifty percent of the female uku attained sexual maturity at 425–475 mm FL, as evidenced by elevated GSI's (Fig. 5) and by the percentage of fish judged mature by visual staging (Table 2). By the time the fish reached the

TABLE 2.—Stage of maturity, compared by 50 mm fork length (FL) size classes, for uku and onaga sampled during their respective spawning seasons.

Uku			Onaga		
FL (mm)	*N*	Percentage mature	FL (mm)	*N*	Percentage mature
275–324	2	0	475–524	11	9
325–374	1	0	525–574	15	7
375–424	2	0	575–624	12	33
425–474	3	66	625–674	4	25
475–524	12	100	675–724	13	77
525–574	21	100	725–774	13	92
575–624	18	95	775–824	16	100
625–674	20	95	825–874	6	100
675–724	15	94	875–925	5	100
725–774	4	100			
775–824	5	100			

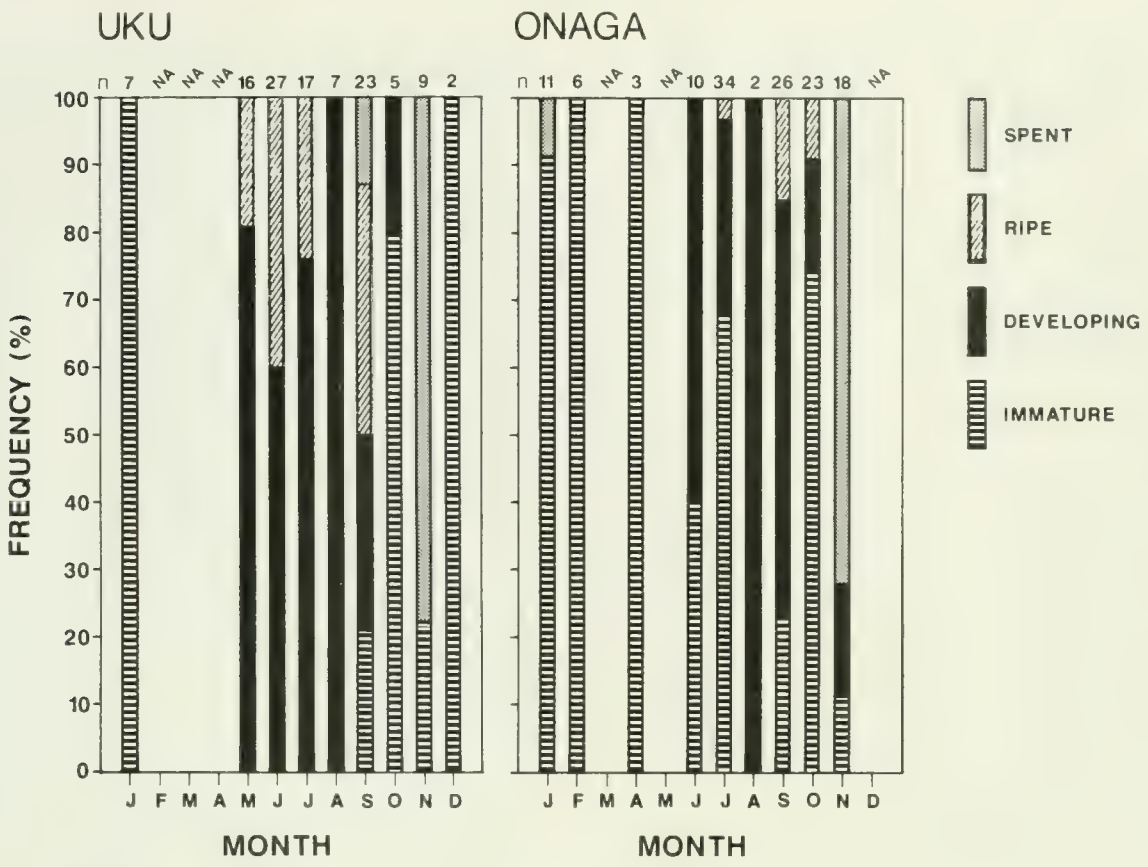


FIGURE 4.—Monthly percentages of uku and onaga ovaries at various stages of development determined by visual staging methods. N = number of samples per month.

500 mm size class, 100% were mature. The smallest uku with vitellogenic (stage II) ovaries during the spawning season was 429 mm FL (1.27 kg), which is 41.7% of the maximum length (MAXLEN) recorded for the study animals. The smallest individual with ripe (stage III) ovaries was 477 mm FL (1.82 kg) or 46.4% of the MAXLEN. The predicted value of L_{50} obtained from the logistic fit of percentage mature on FL (Fig. 6) was 449 mm FL (a = −0.3444, b =

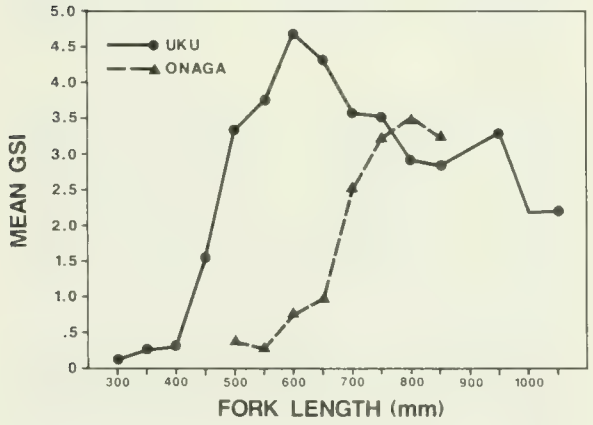


FIGURE 5.—Mean gonosomatic index (GSI) plotted by 50 mm FL intervals for female uku and onaga sampled during their respective spawning seasons.

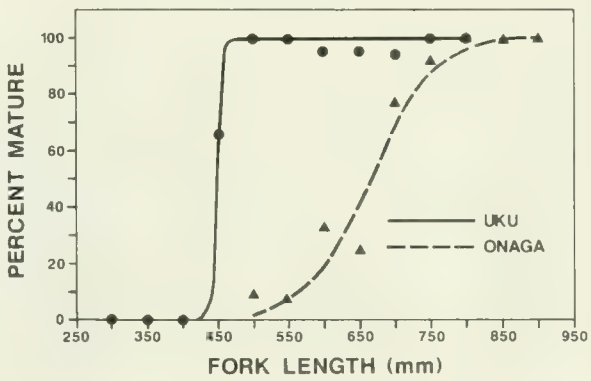


FIGURE 6.—Proportion of sexually mature female uku and onaga within each size class, plotted with the predicted proportion of mature females.

154.31). Interesting to note was the propensity for decreasing mean GSI's in uku larger than 600 mm FL (Fig. 5).

In contrast, the smallest mature onaga was 522 mm FL (2.22 kg) or 53.9% MAXLEN, and ripe individuals were not encountered until 605 mm FL (3.22 kg) or 62.4% MAXLEN. The predicted value of L_{50} obtained from the logistic fit of percentage mature on FL was 663 mm FL ($a = -0.0233$, $b = 15.462$; Fig. 6), and 77% of the onaga in the 675–725 mm FL class were found to be at stage II of development or beyond (Table 2). Onaga spawned over a narrower size range (600–900 mm FL; Fig. 5) compared with uku (450–1,050 mm FL; Fig. 5).

Histological examination of ovaries indicated that both species follow a similar pattern of development (Fig. 7). The progression from oogonia to hydration is typical of snappers and has been covered in detail by Crossland (1977) and Wallace and Selman (1981). Postovulatory follicles were not identifiable in tissue sections from ripe (stage III) ovaries of either species. None of the immature (stage I) ovaries examined histologically showed signs of atresia, indicating that these fish had not previously spawned. Identifiably atretic individuals in later stages of development were not observed until the end of the spawning season.

Spawning Frequency and Pattern of Egg Release

The size-frequency distributions of oocyte diameter were constructed for ovaries of uku caught during the spawning season, using the volumetric method, and were found to be polymodal, suggesting that uku may release multiple egg batches (Fig. 8a). All ovaries possessed a

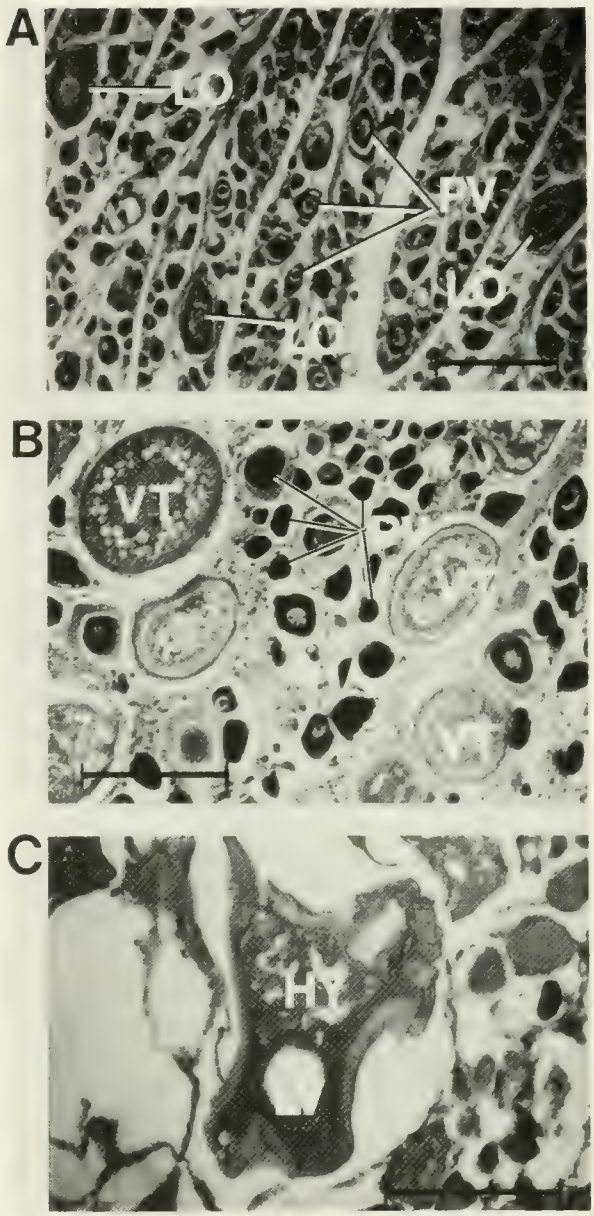
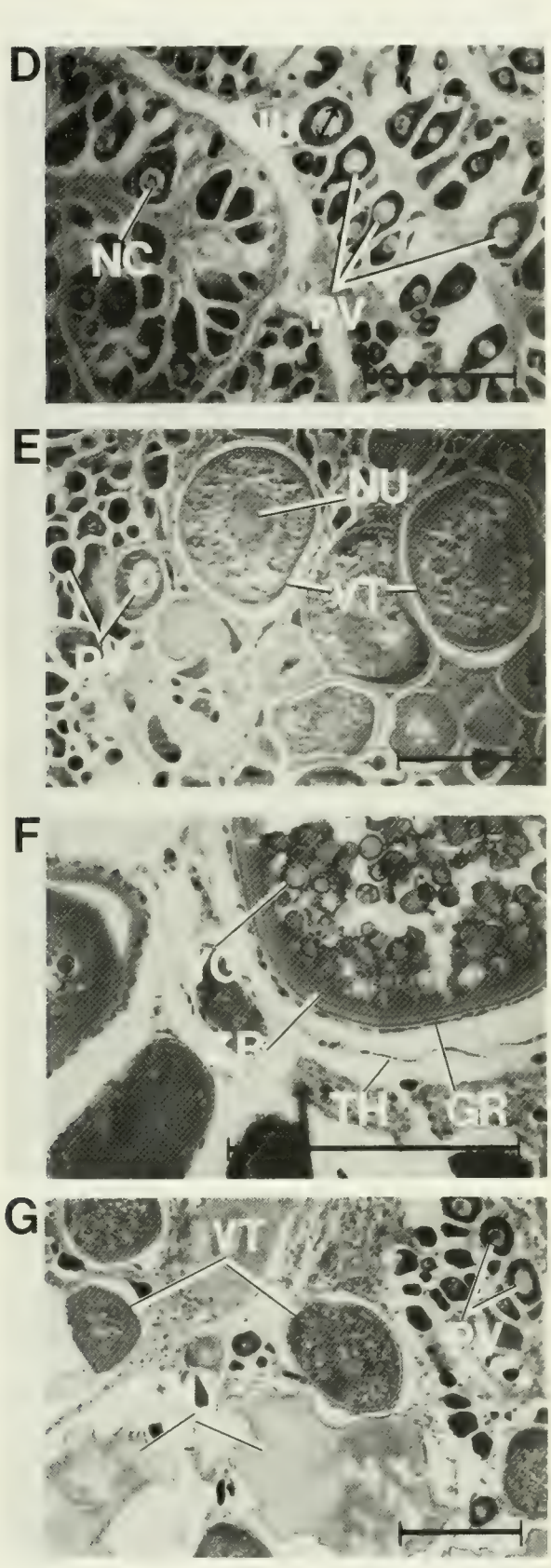


FIGURE 7.—Photomicrographs showing transverse histological sections of uku and onaga ovaries in various stages of development. Scale bars represent 0.10 mm. A. Early developing uku (386 mm FL) ovary classified as juvenile (stage I) containing numerous previtellogenic (PV) oocytes. Larger oocytes (LO) have reached the lipoid or yolk vesicle stage, just prior to vitellogenesis. B. Developing (stage II) uku (525 mm FL) ovary. Shown are previtellogenic (PV) and vitellogenic (VT) oocytes. C. Ripe (stage III) uku (541 mm FL) ovary with hydrated (HY) oocytes. Lipoid vesicles have fused to form a single mass (LV). D. Juvenile (stage I) onaga (506 mm FL) ovary consisting of previtellogenic (PV) oocytes with large central nucleus (NU) containing numerous nucleoli (NC). E. Developing (stage II) onaga (753 mm FL) ovary showing numerous mature oocytes in different stages of vitellogenesis (VT). F. Enlargement of a developing onaga ovary. Shown are granulosa (GR) and thecal (TH) cell layers, zona radiata (ZR), and yolk granules (YG). G. Ripe (stage III) onaga (605 mm FL) ovary showing hydrated (HY), vitellogenic (VT) and previtellogenic (PV) oocytes.



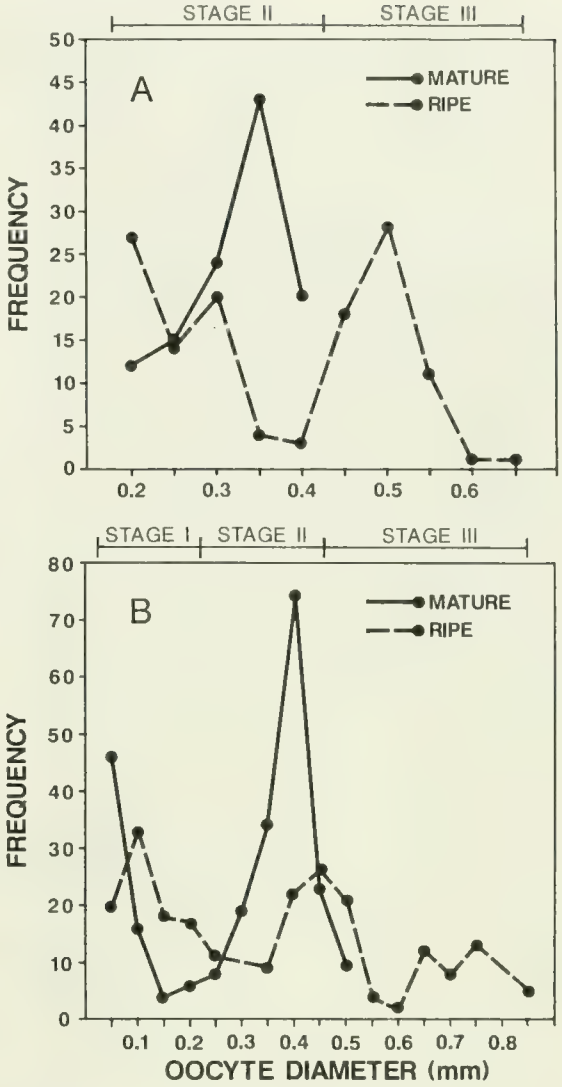


FIGURE 8.—Size-frequency distributions of uku ovaries in various stages of development (cf. Table 1) preserved in (A) Gilson's fluid and (B) Bouin's fluid. Each distribution shown represents a single ovary.

mode of immature oocytes not represented in the figure. Stage II ovaries contained a mode of oocytes at 0.30–0.35 mm, representing various stages of vitellogenesis, while stage III ovaries included this developing mode and another mode (0.50 mm) nearing hydration. A large amount of variation was noted in the relative frequency of oocytes in the most advanced mode of the stage III ovaries. Similar results were exhibited for size-frequency distributions of uku ovaries constructed by the cork borer method. This method allowed delineation of the immature mode as well as the other advanced stages (Fig. 8b). Additional evidence that multiple batches of

oocytes ripen and are successively spawned was indicated by the wide range in GSI values calculated for both species during the spawning season.

Sex Ratio

The sex ratio of male to female uku was 1.05:1 (51.2% males, $N = 559$ individuals combined). A chi-square goodness of fit test suggested that this ratio was not significantly different from the expected 1:1 ratio ($\chi^2 = 0.302$, $P > 0.05$). By examining sex ratio at 50 mm FL intervals, independence was determined and the percentage of females was shown to decrease between the 600 and 750 mm FL categories from 50.0 to 40.9%, then increase 65.5% at 800 mm FL before reaching 100% beyond 900 mm FL. Based on two-way contingency table analysis, the percentage of females caught increased significantly towards the end of the spawning season (September–October; Table 3). Males were caught in higher percentages in the spawning months from May to July.

DISCUSSION

The spawning season for both uku and onaga extends throughout the summer months in Hawaii, as evidenced by the advanced condition of the ovaries and the peaks in ova diameters and GSI values during this period. This pattern has been reported in Hawaii for other snapper species, including *E. carbunculus* (Everson 1984) and *P. filamentosus* (Kikkawa 1984). Spawning activity also occurs during the austral summer for populations of *A. virescens* from New Caledonia (Fourmanoir and Laboute 1976) and East Africa (Talbot 1960; Nzioka 1979). Likewise, peak summer spawning with intermittent activity throughout the rest of the year seemed to be the pattern for *E. coruscans* in Vanuatu (Brouard and Grandperrin 1985). The seasonal peak in spawning activity may be most closely tied to increases in water temperature and day length, as suggested by Walsh (1987) who observed that spawning activity for Hawaiian reef fishes declined rapidly in September to October as maximum water temperatures were reached.

TABLE 3.—Tests of the hypothesis that sex ratio of uku and onaga did not vary significantly from the sample populations during the year. Data are pooled by 2 mo intervals for samples collected in 1984–87 (df = 5).

	Uku			Onaga		
Month	*N*	Percentage female	Contribution to total χ^2	*N*	Percentage female	Contribution to total χ^2
Jan.–Feb.	15 } 17			56	37.5	0.277
Mar.–Apr.	2 }	47.0	0.027	19	15.8	4.976
May–June	359	46.5	0.776	23	60.9	3.771
July–Aug.	88	43.0	1.637	76	47.4	1.292
Sept.–Oct.	69	63.8	6.153	130	33.9	2.719
Nov.–Dec.	28	64.3	2.673	62	41.9	0.174
Total			11.266*			13.209*

* = $P < 0.05$.

The sex ratio of male to female onaga differed significantly ($\chi^2 = 8.99$, $P < 0.05$) from 1:1 in favor of males (61.4%, $N = 347$ individuals combined). The overall ratio of males to females was 1.59:1. There was a significant preponderance of males within the 50 mm FL intervals from 600 to 750 mm. However, females predominated above 850 mm FL, reaching 100% of the individuals in the 950 mm FL category. The two-way contingency table analysis suggested that sex and month of capture were not independent (Table 3).

This pattern would ensure optimum temperature conditions for developing larvae. A similar post-summer spawning decline associated with changing local environmental conditions was noted by Grimes and Huntsman (1980) for *Rhomboplites aurorubens* from North and South Carolina and by Everson (1984) for *E. carbunculus*. The extension of onaga's spawning season into November, with a peak in October, may reflect that the genus *Etelis* is restricted to much greater depths than are the other reef-associated lutjanid species. Seasonal changes in

temperature and photoperiod are much less pronounced at these depths. In Vanuatu, Brouard and Grandperrin (1985) found that seasonal changes in gonad maturation based on GSI values differed among species inhabiting discrete depths.

Grimes (1987) has suggested two distinct spawning patterns for snappers. One is a restricted pattern with spawning centered around the summer months, typical of species associated with continental habitats where peaks in production cycles occur because of nutrient run-off resulting from high rainfall. The opposing pattern is characterized by year-round spawning with peaks occurring in spring and fall, a pattern thought to be typical of less productive insular populations. Grimes (1987) has noted that Cuba and New Caledonia are large islands that follow the continental pattern, with spawning peaks arising during periods of high rainfall. *Etelis carbunculus* (Everson 1984) and *P. filamentosus* (Kikkawa 1984) have also been reported to follow a restricted spawning pattern in the Northwestern Hawaiian Islands. Both uku and onaga in our study also followed the restricted spawning pattern associated with continental habitats. Spawning took place over a protracted period centered around the summer months. Neither species was found in spawning condition at any other time of the year. Since temporal primary production cycles exhibit little seasonal variation throughout the Hawaiian Archipelago (Bienfang and Szyper 1981; Bienfang et al. 1984), the basis for this restricted pattern observed for uku and onaga is unclear. Apparently, the seasonal changes in day length and water temperature in Hawaii provide adequate spawning stimuli.

Interspecies differences in size at sexual maturity also were noted. The slope of the logistic curve fitted to the size at sexual maturity data was considerably steeper for uku compared with onaga (Fig. 6). Uku matured at 450–500 mm FL, with nearly 100% mature above 550 mm FL, and onaga matured at 550–800 mm FL, with 100% mature at 850 mm FL. Size at sexual maturity differed between species in terms of the percentage of MAXLEN at which maturity occurred. Uku began maturing at about 429 mm FL or 42% of their MAXLEN, whereas onaga began maturing at about 522 mm FL or 54% of their MAXLEN. Talbot (1960) reported that male and female *A. virescens* of East Africa reached maturity at 410 mm SL (51%) and 465 mm SL (58%), respectively. *Aprion virescens* off Vanuatu matured at 440 mm FL, a figure that Brouard and Grandperrin (1985) calculated from a MAXLEN coefficient of 57.6%, which was based upon the average values obtained from 34 tropical fish species from the west coast of Africa. The same coefficient, applied to Vanuatu populations of *E. coruscans*, indicated that sexual maturity was reached at 470 mm FL, although developmental staging data obtained for this species revealed that mature fish were first sampled at 330–380 mm FL. The actual size at which maturity commenced in all of these locations agreed closely with our data for uku in Hawaii, while the percentage of MAXLEN values differed considerably. However, Hawaii and Vanuatu populations of onaga matured at substantially different sizes.

Disparities in size at sexual maturity between areas may reflect differences in resource utilization and growth allocation. Grimes (1987) calculated the average percentage of MAXLEN at which sexual maturity occurred for lutjanid populations occupying similar zoogeographic locations and habitats. Insular and continental populations had average MAXLEN values of 51 and 43%, respectively, while the deep (> 91 m) and shallow (< 91 m) species were calculated at 49 and 43%. The MAXLEN value of 42% calculated for the study population of uku indicates that this species fits the shallow, continental pattern. As previously mentioned, onaga are found at much greater depths and therefore seem to be less influenced by continental effects than uku. These observations are substantiated by the fact that the MAXLEN value of 54% calculated for onaga conforms closest to the deep, insular pattern reported in Grimes (1987). He reasoned that these anomalies may result from regional differences in food production. Fish from a relatively resource-rich environment may mature at a proportionally smaller size than fish in less productive habitats. He further speculated that selection may favor maturation at a larger maturing size in insular regions because the cost of year-round spawning may be higher in these areas.

Estimates of von Bertalanffy growth parameters, derived from weight-frequency distributions for uku and onaga landed in Hawaii in 1984–86, indicate that uku mature at about ages 4–5 (429 mm FL), while onaga begin maturing at ages 5–6 (522 mm FL) (Ralston and Kawamoto, fn. 1). In the same study, Ralston and Kawamoto (fn. 1) calculated the size at entry to the fishery

as 650 mm FL for uku and 450 mm FL for onaga in the main Hawaiian Islands, indicating that, for onaga, the present fishery is capturing individuals that have not yet reached sexual maturity. Continuing this practice could lead to a serious decline in spawning stock biomass (Polovina 1987).

Sex ratio also differed between the two species. The ratio of male to female uku was judged not significantly different from the expected ratio of 1:1. In contrast, the onaga sex ratio was significantly different from unity in favor of males. Females dominated in the larger size classes for both species. The preponderance of large females has also been reported for other snapper species, including *Lutjanus synagris* (Reshetnikov and Claro 1976), *R. aurorubens* (Grimes and Huntsman 1980), and *E. carbunculus* (Everson 1984). This phenomenon is thought to be due to differential mortality of the sexes rather than to growth (Wenner 1972; Grimes and Huntsman 1980). The preponderance of male onaga in the smaller size ranges is more difficult to explain and may reflect intersexual behavioral differences. If smaller males feed more aggressively, they would be overly abundant in the catch. Differences in feeding behavior may also explain monthly variations in sex ratio reported for both species. The ratio of female uku increased markedly at the close of the spawning season, suggesting a heightened vulnerability to the fishing gear owing to what may be greater nutritional demands of postspawning females. Seasonally, the largest catch of uku occurs in summer (May–October), when fish are thought to form spawning aggregations (Ralston, fn. 2).

Numerous investigators have suggested that snappers are multiple spawners, based upon the presence of multiple size modes of developing oocytes (Min et al. 1977; Grimes and Huntsman 1980; Everson 1984; Kikkawa 1984; Grimes 1987). Other evidence reported as substantiating this phenomenon has been the wide variations exhibited in GSI's of *L. griseus* (Starck and Schroeder 1970) and *R. aurorubens* (Grimes and Huntsman 1980) during the spawning season. Ralston (1981) suggested that *P. filamentosus* is a multiple spawner because the ovaries of ripe females make up only about 4% of the total body weight, a relatively small percentage compared with that of a single spawning temperate species. These observations, the presence of multiple size modes of developing oocytes and the wide variations in GSI's, were noted for uku and onaga and suggested that these species also spawn repeatedly during the spawning season. Although it has been documented that the oocyte size-frequency distribution of many snapper species contains two or three distinct modes, the exact number of batches spawned per season is rarely reported. This is because the process of recruitment from the undifferentiated oocyte pool is dynamic and difficult to characterize (Grimes 1987).

Much of the above evidence is largely contingent on the assumption that multiple oocyte modes continue to develop and are successively spawned. Foucher and Beamish (1980) observed that, for Pacific hake, *Merluccius productus*, from the Strait of Georgia, oocyte development was multimodal during the spawning season, suggesting multiple spawning for this species. Histological examination of the ovaries revealed, however, that only the largest batch became hydrated and was spawned and all remaining residual yolked oocytes were resorbed. More direct evidence for this mode of spawning, as well as the delineation of the number of batches spawned, has been obtained through the process of identifying and ageing postovulatory follicles in species that exhibit these multiple modes of oocyte development. This method has been used to estimate spawning frequency in several engraulid species (Hunter and Goldberg 1980; Hunter and Macewicz 1980, 1985; Alheit et al. 1984; Parrish et al. 1986; Clarke 1987) and also for the skipjack tuna, *Katsuwonus pelamis* (Hunter et al. 1986). Ageing postovulatory follicles seems to work well for species normally found in large aggregations or schools but has yet to be applied to snappers. The ageing method using postovulatory follicles may be more difficult to apply to such species as snappers, which are known to occur in fewer numbers. Although our study attempted to identify postovulatory follicles in natural populations of uku and onaga, they could not be positively identified or aged. Future studies will have to address this problem, since the delineation of spawning frequency is important for accurate fecundity estimates.

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Larval Development of the Australian Devilfish, *Gymnapistes marmoratus* (Teleostei: Scorpaenidae)

Francisco J. Neira

ABSTRACT: The larval development of the devilfish, *Gymnapistes marmoratus*, is described from material collected in the Swan and Peel-Harvey Estuaries in southwestern Australia. Larvae of *G. marmoratus* examined (2.6–9.3 mm BL) are pelagic and characterized by a deep and compressed, lightly pigmented body; a moderately short gut; 29 myomeres; complex head spination; and large, pigmented fan-shaped pectoral fins which form early in development. Notochord flexion occurs between 4.8 and 6.0 mm BL and transformation between 6.8 and 10.9 mm BL.

The majority of head spines in *G. marmoratus* form before the postflexion stage. These include parietal, supraocular, preopercular, nasal, pterotic, posttemporal, and some suborbital spines. The suborbital stay develops after flexion; the nuchal and three of the anterior preopercular spines disappear in juveniles. The caudal complex of larval *G. marmoratus* includes well-fused hypural elements 1 and 2 and hypural elements 3 and 4, a reduced fifth hypural bone, and a parhypural element.

In addition to larval development, comparisons with similar taxa and the occurrence of the larvae in the Swan Estuary are discussed.

Scorpaeniform fishes are represented in southwestern Australia by one marine species of each of *Centropogon*, *Scorpaena*, *Maxillicosta*, *Gymnapistes*, and *Glyptauchen* and three of *Neosebastes* (Hutchins and Thompson 1983; Hutchins and Swainston 1986). The larval stages of none of these genera have been described except for those of *Scorpaena*, which were described from larvae caught elsewhere (see Moser et al. 1977; Washington et al. 1984a). The present paper describes for the first time the larval development of the sole species of the genus *Gymnapistes*, *G. marmoratus*, using material collected in the Swan and Peel-Harvey Estuaries in southwestern Australia. This paper also includes information on the occurrence and distribution of the larvae in the Swan Estuary.

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The devilfish, *Gymnapistes marmoratus*, also known as the soldier fish or South Australian cobbler, is a marine species common in seagrass beds of coastal embayments and estuaries of southern Australia. It occurs between southern Sydney in New South Wales and Fremantle in Western Australia and occurs also in Tasmania (Hutchins and Thompson 1983; Last et al. 1983; Hutchins and Swainston 1986). Juveniles are relatively common in both the lower Swan Estuary and the Peel Inlet, in southwestern Australia (Chubb et al. 1979; Potter et al. 1983).

The population of *G. marmoratus* studied by Grant (1972) in the D'Entrecasteaux Channel, southern Tasmania, spawned at the beginning of spring at approximately two years of age. In the Gippsland Lakes, Victoria, the adults apparently spawn over an extended period with a peak in winter (Ramm 1986). Larvae of this species have been collected from July to October in Port Phillip Bay, Victoria, with peak abundance occurring in August (Jenkins 1986).

MATERIALS AND METHODS

Collection of Larvae

Larvae of *G. marmoratus* were obtained from plankton samples collected monthly during 1986 in the lower Swan Estuary (lat. 32°04′S, long. 115°44′E). Samples were obtained at night using 0.6 m diameter paired bongo nets, with 0.5 mm mesh, which were towed horizontally 0.5 m below the surface for 10 minutes. Transforming and juvenile *G. marmoratus* were caught in the Peel-Harvey Estuary (32°35′S, 115°45′E) using a 3.0 mm mesh beach seine. Samples were fixed in 10% formalin and specimens were stored in 70% alcohol.

Material Examined

A total of 22 larvae, ranging in body length (BL) from 2.6 to 6.8 mm, were used to describe pigmentation, morphometrics, and meristics. One transforming larva (9.3 mm BL) and seven

benthic juveniles, ranging from 10.9 to 16.8 mm BL, were also examined. Ten representative larval *G. marmoratus* were deposited in the Western Australian Museum (Perth) under the catalogue number P-29814-001.

Measurements and Counts

Larval and juvenile *G. marmoratus* were measured to the nearest 0.1 mm using a Wild M8[1] dissecting microscope fitted with an ocular micrometer. Terminology and body measurements of larvae follow Leis and Rennis (1983). All lengths except body length (BL, mm), i.e., the notochord length in preflexion and flexion larvae and the standard length in postflexion larvae, are expressed as a percentage of body length. Myomere counts and fin ray counts of paired fins were made on the left side of the body. Pigment refers to melanin. Illustrations were done with the aid of a drawing tube.

Six larval, one transforming, and three juvenile *G. marmoratus* were cleared and double stained for bone and cartilage following the technique of Potthoff (1984), as modified from Dingerkus and Uhler (1977). These specimens were used to count fin rays and vertebrae, to determine the sequence of bone ossification, and to describe the development of both the head spines and the caudal complex. The term "ossified" refers solely to structures stained positively for bone. The terminology used for describing the head spination and the caudal complex was modified from that of Washington et al. (1984a) and Feeney (1986) respectively.

RESULTS

Identification

Larvae were identified as scorpaenids by the well-developed head spination, the continuous dorsal fin, and the large, fan-shaped, pigmented pectoral fins (Leis and Rennis 1983). Specimens were initially assembled in a series according to the degree of formation of the pectoral fins which, when fully formed, have 11 fin rays. Large specimens were identified as *G. marmoratus* by dorsal and anal fin ray counts of XIII, 9 and III, 6 respectively and the elongate infraorbital spine (Scott et al. 1980; Last et al. 1983). Fin ray counts, head spination, and body pigment were used to link larvae and juveniles.

Description of Larvae

Larvae of *G. marmoratus* are pelagic prior to transformation. Larvae are initially elongated, becoming deep-bodied (12–36% BL) and laterally compressed with development (Table 1, Figs. 1, 2). The smallest larva illustrated (3.3 mm, Fig. 1A) possesses pectoral fin buds and a dermal sac enclosing most of the body but has neither head spines nor traces of yolk sac. The head length increases from 13% BL in preflexion larvae to 38% BL in postflexion larvae (Table 1). The mouth is formed by 3.3 mm and teeth appear along the premaxilla and dentary at 6.8 mm. The gut is coiled and short in small larvae. The preanal length increases from 35% BL in preflexion larvae to 61% BL in postflexion larvae (Table 1, Figs. 1, 2). There is a moderate gap between the anus and the origin of the anal fin in postflexion larvae (Fig. 2). A prominent swimbladder becomes visible above the gut from about 3.3 mm, but it is no longer externally visible by 10 mm.

Larval *G. marmoratus* possess 29 myomeres. Double-stained specimens have 28 vertebrae (Table 2). Notochord flexion commences by 4.8 mm and is complete by 6.0 mm. Transformation from the pelagic larva to the benthic juvenile occurs between 6.8 and 10.9 mm (Fig. 2A, B).

Fin Development

The development of fins in larval and juvenile *G. marmoratus* is summarized in Table 2. Pectoral fins develop very rapidly, attaining a length of 44% BL in postflexion larvae (Table 1, Fig. 2A). Incipient fin rays of the pectoral fin are visible by 3.3 mm, and all 11 fin rays are formed by 4.7 mm. The caudal fin starts to form by 4.6 mm and is completely developed shortly after notochord flexion is complete (Figs. 2A, 4C). The dorsal and anal fin anlagen appear by 5.0 mm, i.e., prior to completion of notochord flexion, and the rays start to form sequentially from tail to head. Rays and spines, both dorsal (XIII, 9) and anal (III, 6), are developed by 9.0 mm (Table 2). Pelvic buds are visible by 4.8 mm and fin rays are formed by 9.3 mm.

Pigmentation

Larval *G. marmoratus* are lightly pigmented prior to transformation. In preflexion larvae, the

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Morphometric measurements for larval, transforming, and juvenile *Gymnapistes marmoratus*. Body intervals are expressed as a percentage of body length; n = number of individuals. Means and standard deviations (in parentheses) are given when $n > 1$. Blanks indicate character is absent. Individuals indicated with * and ** correspond to a transformed larva and juveniles respectively. Individuals between dashed lines were undergoing notochord flexion.

Body length (mm)	n	Head length	Snout length	Eye diameter	Body depth at pectoral fin base	Pectoral fin length	Preanal length	Predorsal fin length
2.6	1	17.7	3.4	7.6	12.7	7.6	38.4	.
2.7	1	13.7	2.8	7.9	14.4	15.2	36.1	.
3.3	1	17.8	2.9	7.5	17.8	19.0	38.7	.
4.0	1	19.6	4.6	7.6	16.6	20.6	40.2	.
4.6	1	19.6	3.8	7.2	15.0	27.8	35.2	.
4.7	1	22.4	4.7	7.1	17.5	31.2	41.6	.
4.8	1	23.9	5.7	7.8	23.5	32.9	45.7	.
5.0	1	25.2	4.3	8.3	25.0	35.6	47.0	54.8
5.1	2	23.4(0.10)	5.7(0.50)	7.6(0.05)	21.4(1.25)	35.2(0.15)	45.4(2.50)	58.6(n = 1)
5.2	1	24.3	6.0	7.1	21.0	33.7	45.5	.
5.3	1	23.9	5.4	8.1	22.0	33.1	49.3	56.1
5.5	1	30.4	7.5	8.5	24.3	34.0	49.6	59.6
5.7	1	29.2	6.5	8.7	24.6	38.0	54.5	58.5
5.8	1	32.0	8.8	8.4	27.6	42.4	50.7	28.9
5.9	1	27.6	5.3	8.7	24.9	35.7	51.6	57.2
6.0	2	30.0(0.49)	7.9(0.75)	7.5(0.00)	24.9(1.33)	34.6(0.08)	51.6(1.08)	59.8(0.00)
6.1	1	32.4	7.0	8.5	26.6	35.7	57.8	32.1
6.2	2	29.6(2.45)	7.5(0.75)	8.1(0.10)	27.6(0.95)	34.6(0.60)	54.7(1.45)	28.8(0.95)
6.8	1	32.6	9.0	8.4	27.7	43.9	57.2	30.6
9.3*	1	33.3	7.4	9.8	30.5	31.2	62.8	29.0
10.9**	1	34.0	6.8	9.9	32.3	27.1	63.1	27.8
13.9**	1	35.6	6.9	10.2	33.9	30.3	60.4	24.5
14.1**	1	36.0	8.7	9.2	33.8	32.6	64.1	30.3
15.1**	1	37.6	6.3	10.9	35.7	34.7	60.3	23.9
15.7**	1	36.6	6.7	10.3	31.8	29.2	60.5	23.2
15.8**	1	36.7	8.2	9.7	36.7	29.8	61.6	23.1
16.8**	1	38.6	7.5	10.1	31.9	30.1	61.3	21.7

head has one melanophore at the angle of the lower jaw, one ventral melanophore at the gular area, and a group of internal melanophores at the base of the hindbrain. All of these melanophores are retained (Figs. 1, 2). Melanophores appear on the midbrain by 4.9 mm and develop over the snout, opercular, and gular areas by 6.0 mm.

The dorsal surface of the swimbladder and ventral surface of the gut are pigmented in preflexion larvae. A single row of melanophores occurring along the ventral surface of the gut in small larvae persists throughout development (Figs. 1, 2). Melanophores appear externally on the lateral surface of the trunk by 6.2 mm and expand over the gut area by 9.5 mm (Fig. 2A, B). A single row of 16–22 melanophores is present on the ventral surface of the tail in preflexion larvae, each melanophore spaced about one per myomere. This single row of melanophores becomes double along the anal fin base in postflexion larvae. Pigment appears on the dorsal surface of the body by 5.5 mm and, shortly after, on the lateral surface of the body. Transition from larval to juvenile pigmentation begins by 6.8 mm. Juveniles develop blotches of pigment on the head, trunk, and dorsal and anal fin membranes (Fig. 2B).

Melanophores appear on the pectoral fins by 3.3 mm (Fig. 1A), extend distally on each pectoral ray by 4.6 mm, and remain along the edges of the distal portion of the rays throughout development (Fig. 2A). In larvae over 10 mm, patches of pigment form on the pectoral fin bases and on the fin membranes (Fig. 2B). Melanophores appear on the dorsal and anal fin membranes by 6.0 mm, and patches of pigment form on the membranes of these fins by 10 mm. The

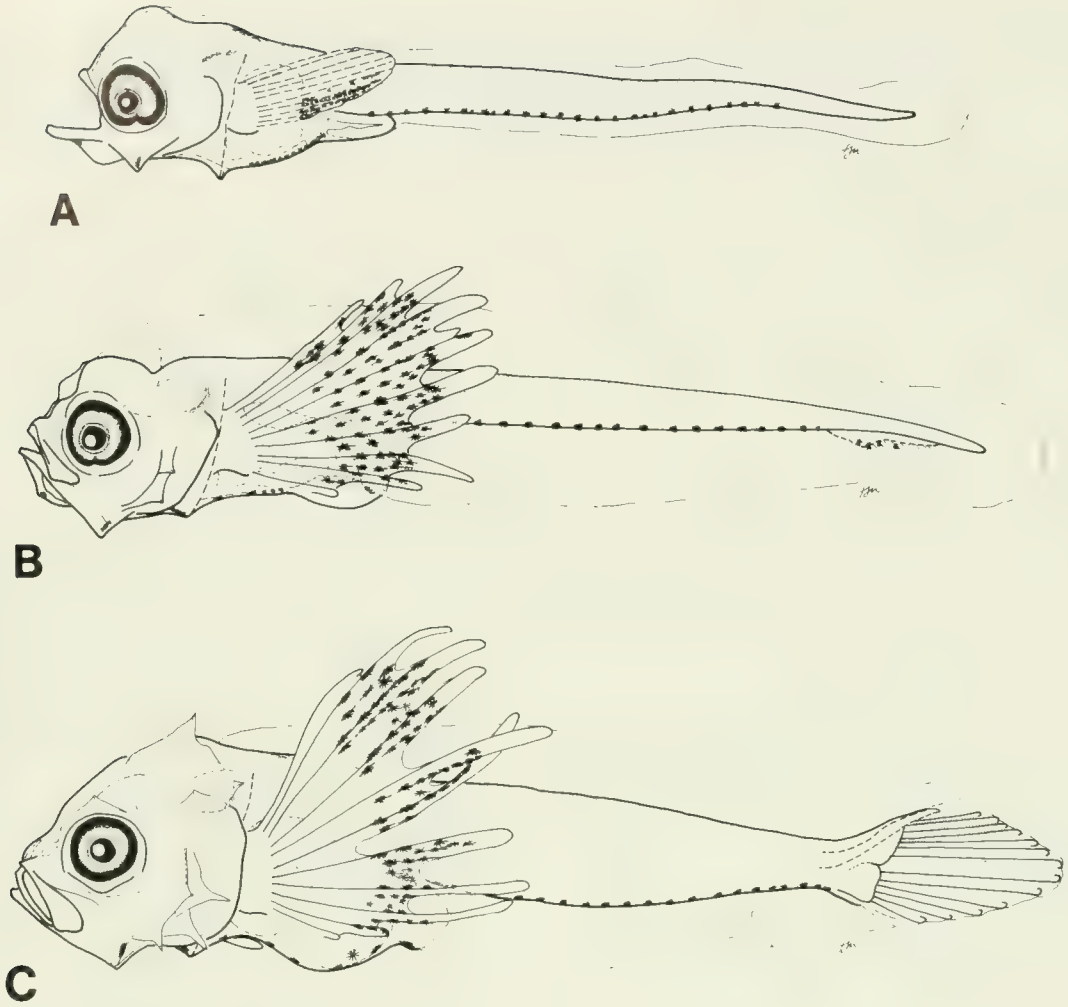

FIGURE 1.—Larvae of the devilfish, *Gymnapistes marmoratus*, caught in the lower Swan Estuary in July 1986. (A) 3.3 mm BL larva. (B) 4.6 mm BL larva. (C) 5.1 mm BL larva; note pelvic fin buds.

TABLE 2.—Fin ray development and vertebral counts in larval, transforming, and juvenile *Gymnapistes marmoratus*. Vertebrae were counted only in cleared and double-stained specimens (denoted by *) in which vertebrae were clearly differentiated. Other blanks indicate character is absent. Pectoral and pelvic fin ray counts were made on the left side of the body. Procurrent fin rays are shown as dorsal/ventral elements.

Body length (mm)	*n*	Stage	Dorsal fin	Anal fin	Pectoral fin	Pelvic fin	Caudal fin rays	Procurrent rays	Vertebrae
2.6	1	Preflexion			bud				
2.7	1	Preflexion			bud				
3.3	1	Preflexion			8				
4.0*	1	Preflexion			10				
4.6	1	Preflexion			10				
4.7*	1	Preflexion			11		9		
4.8	1	Flexion			11	bud	10		
5.0*	1	Flexion	anlage	anlage	11	bud	5+5		28
5.1	2	Flexion	anlage	anlage	11	bud	7+5		
5.2*	1	Flexion	anlage	anlage	11	bud	5+5		28

FIGURE 2.—Larva and juvenile of the devilfish, *Gymnapistes marmoratus*. (A) 6.2 mm BL larva collected in the Swan Estuary in July 1986. (B) 10.9 mm BL juvenile collected in the Peel-Harvey Estuary in August 1985; dashed lines indicate damaged caudal fin.

TABLE 2.—*Continued.*

Body length (mm)	*n*	Stage	Dorsal fin	Anal fin	Pectoral fin	Pelvic fin	Caudal fin rays	Pro-current rays	Verte-brae
5.3*	1	Flexion	8	6	11	bud	6+7	1/0	28
5.5	1	Flexion	8	5	11	bud	7+6	1/0	
5.7	1	Flexion	9	7	11	bud	7+6	1/1	
5.8	1	Flexion	10	7	11	bud	7+6	1/1	
5.9	1	Flexion	9	7	11	bud	7+7	1/2	
6.0	2	Flexion	9–10	7–8	11	bud	7+6	1/2–1	
6.1	1	Postflexion	9	8	11	bud	7+7	2/3	
6.2	2	Postflexion	19–22	III,5	11	bud	7+6	1–2/3	
6.8*	1	Postflexion	21	III,6	11	bud	7+7	3/3	28
9.3*	1	Transforming	XIII,9	III,6	11	I,5	7+7	5/5	28
10.9	1	Juvenile	XIII,9	III,6	11	I,5	7+7	5/5	
13.9	1	Juvenile	XIII,9	III,5	11	I,5	7+7	6/6	
14.1*	1	Juvenile	XIII,9	III,6	11	I,5	7+7	6/5	28
15.1*	1	Juvenile	XIII,9	III,6	11	I,5	7+7	6/5	28
15.7	1	Juvenile	XIII,9	III,6	11	I,5	7+7	6/5	
15.8	1	Juvenile	XIII,9	III,6	11	I,5	7+7	6/6	
16.8*	1	Juvenile	XIII,9	III,6	11	I,5	7+7	7/6	28

caudal fin remains unpigmented throughout development.

Development of Head Spines

Larvae of *G. marmoratus* have complex and well developed head spination (Fig. 3). Two posterior preopercular spines (PPO_2 and PPO_3) appear simultaneously at 4.6 mm (Fig. 1B; see Figure 3 for abbreviations also). Two more posterior preopercular spines (PPO_1 and PPO_4) develop by 5.7 mm and a fifth (PPO_5) by 10 mm. The PPO_1 spine becomes enlarged in juveniles, reaching a relative length of ca. 12% BL (Fig. 3D). Two anterior preopercular spines (APO_2 and APO_3) form by 4.8 mm, followed by a third anterior preopercular spine (APO_1) by 5.4 mm. All spines of both the anterior and posterior preopercular margins merge by 6.8 mm and only the APO_1 spine, the enlarged PPO_1 spine, and the PPO_{2-5} spines remain in juveniles (Fig. 3D).

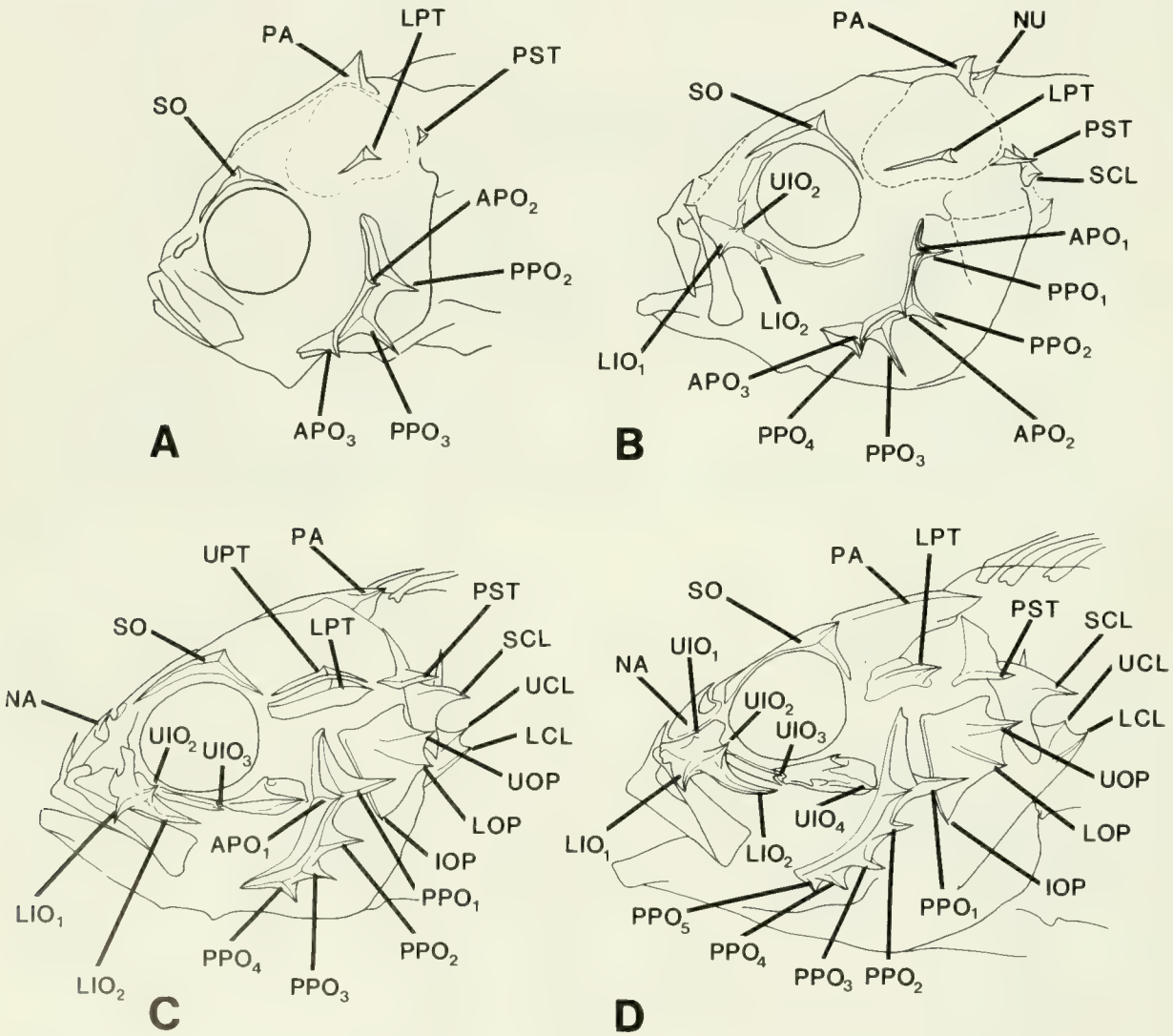

FIGURE 3.—Head spination in cleared and double-stained larval, transforming and juvenile *Gymnapistes marmoratus*. (A) 5.3 mm BL larva. (B) 6.8 mm BL larva. (C) 9.3 mm BL transforming larva. (D) 14.1 mm BL juvenile. Abbreviations: APO_1, 1st anterior preopercular; APO_2, 2nd anterior preopercular; APO_3, 3rd anterior preopercular; IOP, infraopercular; LCL, lower cleithral; LIO_1, 1st lower infraorbital; LIO_2, 2nd lower infraorbital; LOP, lower opercular; LPT, lower pterotic; NA, nasal; NU, nuchal; PA, parietal; PPO_1, 1st posterior preopercular; PPO_2, 2nd posterior preopercular; PPO_3, 3rd posterior preopercular; PPO_4, 4th posterior preopercular; PPO_5, 5th posterior preopercular; PST, posttemporal; SCL, supracleithral; SO, supraocular; UCL, upper cleithral; UIO_1, 1st upper infraorbital; UIO_2, 2nd upper infraorbital; UIO_3, 3rd upper infraorbital; UIO_4, 4th upper infraorbital; UOP, upper opercular; UPT, upper pterotic.

The parietal spines (PA) develop prior to flexion and are retained in juveniles but become blunt. The nuchal spines (NU) appear posterior to the parietal spines by 5.7 mm and disappear by 9.0 mm (Fig. 3C). The lower pterotic (LPT) and supraocular (SO) spines appear simultaneously at 4.8 mm and the posttemporal spine (PST) by 5.1 mm. A small upper pterotic spine (UPT) appears dorsal to the lower pterotic spine (LPT) by 9.0 mm and fuses to the LPT spine by 10.0 mm. All LPT, SO, and PST spines persist in juveniles (Figs. 2B, 3C, D).

The second upper infraorbital (UIO_2) and the first lower infraorbital (LIO_1) spines form simultaneously at 5.5 mm. The second lower infraorbital spine (LIO_2), which forms by 6.8 mm underneath the eye, grows backwards as a recurved hook reaching a relative length of ca. 16.5% BL in juveniles (Fig. 3B, C, D). The nasal (NA), upper and lower cleithral (UCL, LCL), and the upper opercular, lower opercular, and infraopercular (UOP, LOP, IOP) spines form during transformation and remain in juveniles (Fig. 3D).

Development of the Caudal Complex

The development of the caudal complex in larval *G. marmoratus* is illustrated in Figure 4. Three nonossified hypural elements (HY_1, HY_3, HY_4) form at about 4.7 mm ventral to the notochord (N) (Fig. 4A). The third and fourth hypural elements (HY_3, HY_4) fuse to form a plate by 5.3 mm (Fig. 4B), leaving a small fora-

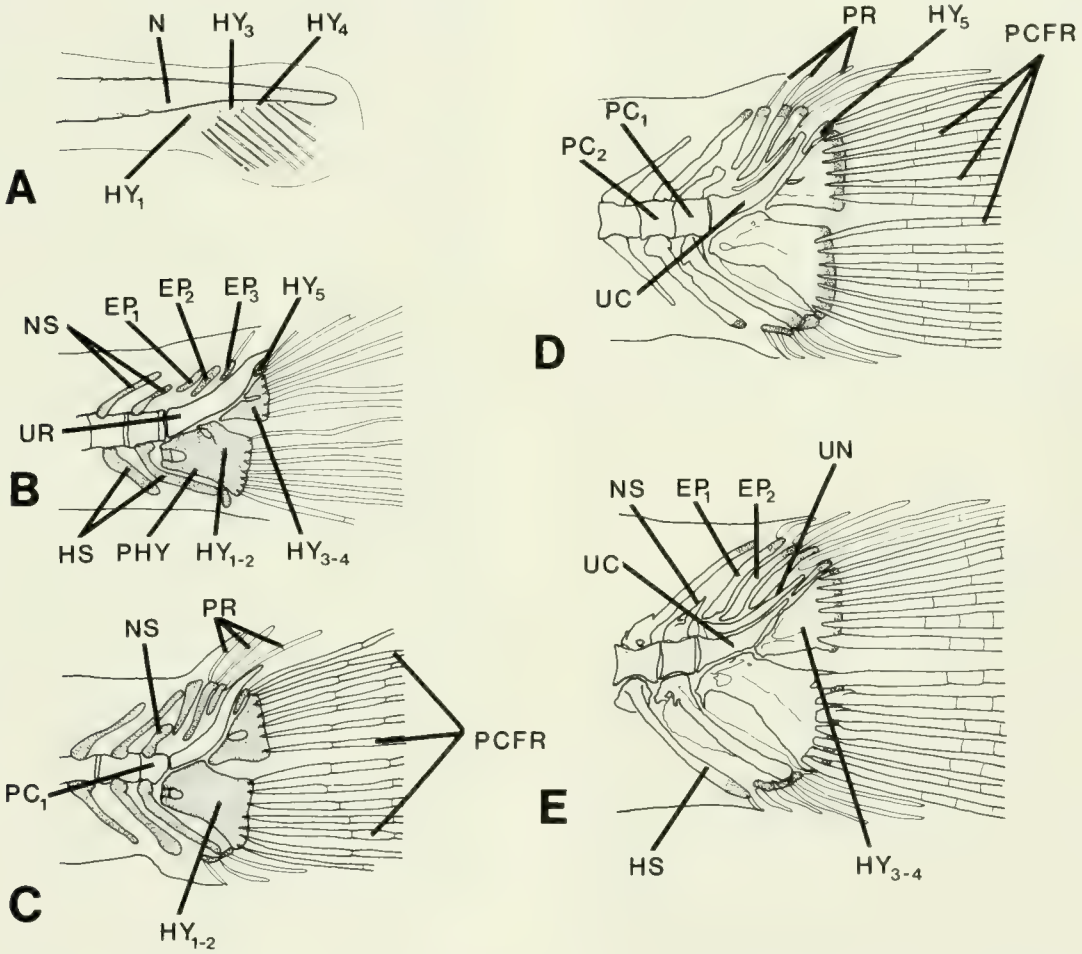

FIGURE 4.—Development of the caudal complex in cleared and double-stained larval, transforming, and juvenile *Gymnapistes marmoratus*. (A) 4.7 mm BL larva. (B) 5.3 mm BL larva. (C) 6.8 mm BL larva. (D) 9.3 mm BL transforming larva. (E) 14.1 mm BL juvenile. Shaded areas represent elements stained with alcian blue. Abbreviations: EP, epural; HS, haemal spine; HY, hypural; N, notochord; NS, neural spine; PC, preural centrum; PCFR, principal caudal fin ray; PHY, parhypural; PR, procurrent ray; UC, ural centrum; UN, uroneural; UR, urostyle.

men which disappears in juveniles (Fig. 4E). A fifth, reduced, hypural element (HY_5) forms ventral to the tip of the notochord by 5.3 mm and remains discrete from the upper hypural plate (HY_{3-4})in juveniles (Fig. 4B, E). Two distinct foramina are visible in the lower hypural plate (HY_{1-2}) by 5.3 mm. The distal foramen results from the fusion between HY_1 and HY_2 elements, whereas the proximal foramen is probably the result of the fusion between the lower plate (HY_{1-2}) and the parhypural element. Only the proximal foramen remains in juveniles (Fig. 4E). One principal caudal fin ray (PCFR) is attached to the uppermost hypural element (HY_5), six to the upper hypural plate (HY_{3-4}), and seven to the lower hypural plate (HY_{1-2}) by 6.8 mm. Both the HY_{1-2} and HY_{3-4} plates ossify by 9.0 mm and remain discrete from each other and from the ural centrum (UC) in juveniles (Fig. 4E).

Three epural elements (EP_1, EP_2, EP_3) appear dorsal to the urostyle (UR) at about 5.3 mm, with a single procurrent ray attached to the EP_3 (Fig. 4B). Ventral procurrent rays appear by 7.5 mm and the number increases to seven dorsal and six ventral procurrent rays by 16.8 mm (Table 2). A uroneural (UN) starts to form dorsal to the ural centrum by 9.0 mm, and it is completely formed by 14.0 mm (Fig. 4D, E). Nonossified neural (NS) and haemal (HS) spines form simultaneously shortly after flexion is commenced and all are ossified by 9.0 mm. The neural spine on the first preural centrum (PC_1) is reduced (Fig. 4, C, E).

DISCUSSION

Comparisons to Subfamilies of the Scorpaenidae

The larval development of *G. marmoratus* follows a similar pattern to that observed in other scorpaenid species (Washington et al. 1984a). The sequence of fin formation in larval *G. marmoratus* parallels that of larvae of the subfamilies Sebastinae and Scorpaeninae, except that the pelvic fins in *G. marmoratus* are completely formed following, rather than prior to, the formation of the anal and dorsal fins. Notochord flexion in larval *G. marmoratus* (4.8–6.0 mm) occurs at similar sizes to that observed in scorpaenine larvae (4.0–6.0 mm) but earlier than in sebastine (6.0–12.0 mm) and sebastolobine (6.0–7.3 mm) larvae (Washington et al. 1984a). In addition, transformation of *G. marmoratus* larvae occurs much earlier (6.8–10.9 mm) than in the larvae of the other three subfamilies (10.0–20.0 mm) (Washington et al. 1984a).

The majority of the head spines of *G. marmoratus* develop before the postflexion stage, as is the case in other scorpaenid larvae. The parietal spines are not as prominent as in sebastine and scorpaenine larvae and lack the serrations usually found in the parietal spines of the larvae of these subfamilies (Washington et al. 1984a). The small nuchal spines, which disappear in juveniles, are excluded from the parietal ridges and never exceed in length those of the parietal spines, as has been observed in other scorpaenine larvae. In addition, all anterior preopercular spines except the APO_1 spine disappear in larval *G. marmoratus* after flexion has been completed; the same spines disappear in sebastine larvae (Washington et al. 1984a). The prominent suborbital stay of larval *G. marmoratus* (LIO_2 spine), which starts to develop after flexion, is venomous in adult specimens (Hutchins and Thompson 1983; Last et al. 1983). In contrast to larval *G. marmoratus*, this suborbital spine is absent or incomplete in sebastine, scorpaenine, and sebastolobine larvae. The absence of a suborbital spine has been suggested as a plesiomorphic condition in Scorpaeniformes (Washington et al. 1984b).

The presence of well-fused hypurals 1 and 2 (lower hypural plate) and hypurals 3 and 4 (upper hypural plate) in the caudal complex of larval *G. marmoratus* represent a derived character in scorpaeniform fish according to Washington et al. (1984b). By contrast, the presence of both a reduced fifth hypural element (HY_5) and a parhypural element represents a plesiomorphic condition, which in turn suggests that this monospecific genus still retains characters that correspond to a more generalized type of scorpaenid. More information is needed, however, on related genera of the Scorpaenidae to provide a more detailed comparison of these characters in larval *G. marmoratus* and to suggest relationships within the suborder Scorpaenoidei.

Distinguishing Larval Characters

Larval *G. marmoratus* can be distinguished from other scorpaenid larvae that occur within its geographical range by the possession of 29 myomeres, the dorsal fin count of XIII, 9, and their large and distinctively pigmented fan-shaped pectoral fins which form early in development. Larvae of *Scorpaena* are distinguished

from *G. marmoratus* by a lower number of myomeres, whereas *Maxillicosta* and *Neosebastes* possess a higher number of pectoral fin rays (18–21) (Scott et al. 1980; Leis and Rennis 1983). Larvae of *Centropogon* and *Glyptauchen* are distinguished from *G. marmoratus* by their possession of a higher number of spines (15–18) in the dorsal fin (Washington et al. 1984b). Juvenile *G. marmoratus* can also be distinguished from other known scorpaenids in the area by their distinctive head spination and scaleless skin (Hutchins and Thompson 1983).

Larvae of *G. marmoratus* can be confused with some platycephalids and triglids, which also have pigmented pectoral fins and well-developed head spination. However, platycephalid larvae have numerous small melanophores scattered over the body surface, depressed heads with flattened snouts, and smaller parietal spines (Leis and Rennis 1983). Triglid larvae can be distinguished from *G. marmoratus* by the depressed profile of their heads and by large pectoral fins in which the lowest three rays become detached during transformation (Washington et al. 1984a).

Occurrence of Larvae in the Swan Estuary

Gymnapistes marmoratus larvae were found in surface waters of the Swan Estuary between July and September 1986, and peak numbers were obtained in July (Neira, unpubl. data). Larvae were collected in the area of the lower Swan Estuary located between 3.0 and 9.0 km upstream from the estuary mouth. The transforming larva and juveniles from the Peel-Harvey Estuary were collected by beach seines in October and August 1985 respectively. The occurrence of larvae and juveniles from both estuaries indicates that a population of *G. marmoratus* from southwestern Australia spawns in late winter and early spring. This spawning period is coincident with that reported in other regions of southern Australia such as Tasmania (Grant 1972), Port Phillip Bay (Jenkins 1986), and the Gippsland Lakes (Ramm 1986).

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New Squat Lobsters (Galatheidae) from the Pacific Ocean: Mariana Back Arc Basin, East Pacific Rise, and Cascadia Basin

Austin B. Williams and Keiji Baba

ABSTRACT: Three species of squat lobsters new to science are described and illustrated. *Munidopsis marianica*, collected with the aid of DSRV *Alvin* from a hydrothermal vent area in the Mariana Back Arc Basin in the western Pacific, is distinguished from a northeastern Pacific species, *M. tuftsi* Ambler, by the erectness of its eye spines and ornamentation of the body, form of telson plates, and spination of dactyls on walking legs. *Munidopsis lignaria*, collected in association with submerged wood with the aid of RV *Yaquina* in trawl samples from the eastern Pacific Cascadia Basin off Oregon and DSRV *Alvin* from the East Pacific Rise off south central Mexico, is distinguished from its nearest congener, *M. ciliata* Wood-Mason, by blunter ornamentation and smaller body size. *Munidopsis granosicorium* from Cascadia Basin is represented by a unique specimen, the carapace of which has a distinctive unspined ornamentation but a much more broadly triangular rostrum and more pronounced anterior elevation than that of its apparent closest relative, *M. follirostris* Khodkina.

On a recent *Alvin/Atlantis II* expedition to the Mariana Back Arc Basin in the western Pacific, 28 dives were made, 6 of them entirely devoted to biology. Those dives focused on 3 active low temperature (10°–25°C) vent sites at which anemones, mollusks, shrimps, squat lobsters, crabs, and other invertebrates were observed or collected (R. Hessler[1]; Hessler et al. 1988). We here describe a new species of *Munidopsis* collected during 3 of the dives.

A subsequent *Alvin/Atlantis II* expedition (Cruise 118, Leg 32) focused on geological exploration of the East Pacific Rise between lat. 10°55′N and 11°55′N. Small fields of past and present hydrothermal activity were found along the axis of this region, and among samples of biological specimens collected from both vent and nonvent environments was a piece of wood colonized by a variety of invertebrates, including a species of *Munidopsis* (see Van Dover 1988). These specimens are identical to specimens taken during extensive collections of benthic megafauna made at stations of the RV *Yaquina* on the Oregon continental margin and nearby abyssal plains from 1962 to 1983 (Ambler 1980; Carney and Carey 1982; Carey[2]). A pattern of stations was sampled to determine the distribution and abundance of mega-epifauna and to study the ecological influence at sea of radionuclides originating from the Hanford (WA) Nuclear Reservation. Collections at these and other study areas in the region were made with a 7.1 m semiballoon otter trawl (1.3 cm mesh) and with a 3 m beam trawl (1.3 cm mesh) equipped with paired odometer wheels (Carey and Heyamoto 1972). We reviewed all of this material and here describe the species as new. Finally, a unique but fragmentary specimen of *Munidopsis* from Professor Carey's sampling program is described.

Specimens studied, except where otherwise indicated, were from the Oregon State University Benthic Invertebrate Museum (OSUBI), Corvallis, OR; the Museum of Comparative Zoology, Harvard University (MCZ), Cambridge, MA; and the Division of Crustacea of the United States National Museum of Natural History, Smithsonian Institution (USNM), Washington, DC. Types of new species are deposited in crustacean collections of the USNM and OSUBI.

Munidopsis marianica New Species

Figures 1, 2*a*, 3*a*, *b*

Material studied.—Western Pacific Ocean,

[1]Robert Hessler, Scripps Institution of Oceanography, La Jolla, CA 92093, pers. commun. September 1987.

[2]A. G. Carey, Jr., College of Oceanography, Oregon State University, Corvallis, OR 97331, pers. commun. September 1988.

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Fishery Bulletin, U.S. 87: 899–910.

Mariana Back Arc Basin. USNM 240198. Holotype ♀ (ovig.). Burke Field, 18°11′N, 144°43′E, 3,680 m, *Alvin* Dive 1837, 28 April 1987, Pilot Salzig, Observers Hessler, France.—USNM 240199. Paratypes, 2 ♀ (ovig.), 1 ♂, same.—USNM 240200. Paratype ♀. Illium, 18°15′N, 144°42′E, 3,620 m, *Alvin* Dive 1829, 14 April 1987, Pilot Tibbets, Observers Craig, Farley.—USNM 240201. Paratype ♀. 18°11′N, 144°43′E, 3,727 m, *Alvin* Dive 1847, 8 May 1987, Pilot Salzig, Observers J. and D. Hawkins; transferred to collection of the Zoological Laboratory, Kyushu University (ZLKU). The material was graciously donated to us by R. Hessler, Scripps Institution of Oceanography, La Jolla, CA.

Measurements in mm.—Holotype ♀ (ovig.), carapace length including rostrum 52.1, margin of orbit to posterior edge of carapace 38.0, maximum carapace width 30.8; same (respectively). Paratypes USNM 240199, ♀ (ovig.) 33.9, 25.6, 21.8, ♀ (ovig.) 36.0, 25.8, 21.1, ♂ 26.2, 19.0, 15.3; USNM 240200, ♀ 40.7, 30.2, 26.0; USNM 240201, ♀ 38.0, 28.1, 23.7.

Description.—Carapace (Fig. 1*a–c*) exclusive of rostrum distinctly longer than broad, moderately arched transversely; anterior and posterior cervical grooves apparent, transverse depression in anterior part of cardiac region. Rostrum almost horizontal, narrow to moderately broad triangular, lateral margin with denticles on distal third, tip exceeding eyestalks by more than their length, variably obscure to distinct dorsal carina bearing obsolescent tiny tubercles that merge into median tubercles on gastric region. Slightly raised concave frontal margin sweeping to antennal spine followed by irregularly oblique margin leading to acutely spined anterolateral angle. Gastric region somewhat inflated but slight posterolateral concavity at either side defining meso-metagastric area; anterior gastric region bearing moderate spine on either side of midline, and lateral to each another variably developed spine in moderately arched transverse row; remainder of gastric region lightly rugose. Anterior branchial region bearing strong anterolateral spine followed by 5 or 6 successively diminishing lateral spines, and scattered moderate tubercles dorsally. Short rugae and obscure tubercles clustered behind juncture of anterior and posterior cervical grooves. Posterior branchial region bearing strong anterolateral angle, sometimes spiniform, and distinct oblique and transverse rugae laterally; rugae with tendency to being transversely continuous across central part of cardiac region. Posterior margin concave, preceded by narrow raised rim with slightly cupped crown. Lateral plate obliquely rugose, projecting anteriorly below antennal peduncle; rugosities on anterodorsal margin minutely serrated, and angular anterior tip bearing minute spine.

Abdomen (Fig. 1*a*) unarmed; transverse ridge of segments 2 and 3 smooth, divided into narrow anterior and broader posterior parts by concave trough, that of segment 4 obsolescent; segments 5 and 6 smooth, 6 slightly raised posteriorly in middle, posteromedian margin strongly produced, overreaching lateral lobe on each side. Telson divided into 8 plates (Fig. 2*a*), length-width ratio 0.79 ± SD 0.052, $n = 6$, midlateral plate markedly convex on distolateral margin.

Eyes (Figs. 1*b*, *c*, 3*a*) moderate in size; well exposed, smoothly ovate cornea cupped within movable broad-based ocular peduncle; peduncle extended into strong mesiodorsal spine directed horizontally or obliquely upward at very low angle and ornamented with tiny, irregular, obsolescent spinules; a much shorter lateral spine near base of cornea; behind that an alate basal process, either acutely spined or multispinose at tip, posterolaterally paralleling concave frontal margin.

Basal article of antennular peduncle with distal margin irregularly crenulate; slender dorsolateral carina continued into anterior spine, below it a broader anterior spine directed obliquely laterad, flanked by inflated surface bearing cluster of irregular small spines or spinules; mesiodorsal spine much smaller. Antennal peduncle with fixed basal article extended into stout, flat ventral spine with subdivided mesial margin and shorter, sometimes crenulate, lateral spine; succeeding articles short, second bearing appressed lateral angle, third with serrate distal margin, fourth with scalloped distal margin.

Third maxilliped (Fig. 1*d*) with ischium shorter than merus; bearing mesial crest armed with finely uniform, evenly spaced corneous tipped spines and a distodorsal spine. Basis with 3 or 4 corneous spines similar to and in line with crest on ischium. Merus with 6 irregular acute spines on flexor margin and strong spine at distodorsal corner. Carpus, propodus, and dactyl folded on merus-ischium and about as long as those 2 articles together, flexor surface of each bearing dense setation mesially, and distally on propodus

and dactyl. Sternite at base of third maxilliped (Fig. 1*e*) forming apposed lobe at either side of midline, outline of each irregularly polygonal but with anteromesial process irregularly serrate on margin and divergent.

Epipod on coxa of first pereopod (cheliped), but rudimentary on left side and absent on right side of paratype USNM 240201.

Chelipeds (Fig. 1*f*) subequal, with many spines and fewer rugosities tending to arrangement in longitudinal tracts; ischium with mesial row of 8 acute spines, irregular smaller spines on distoventral margin, and smaller spines and rugosities ventrally; merus reaching end of rostrum, bearing row of 7 mesial spines, terminal one strongest, about 10 spines along

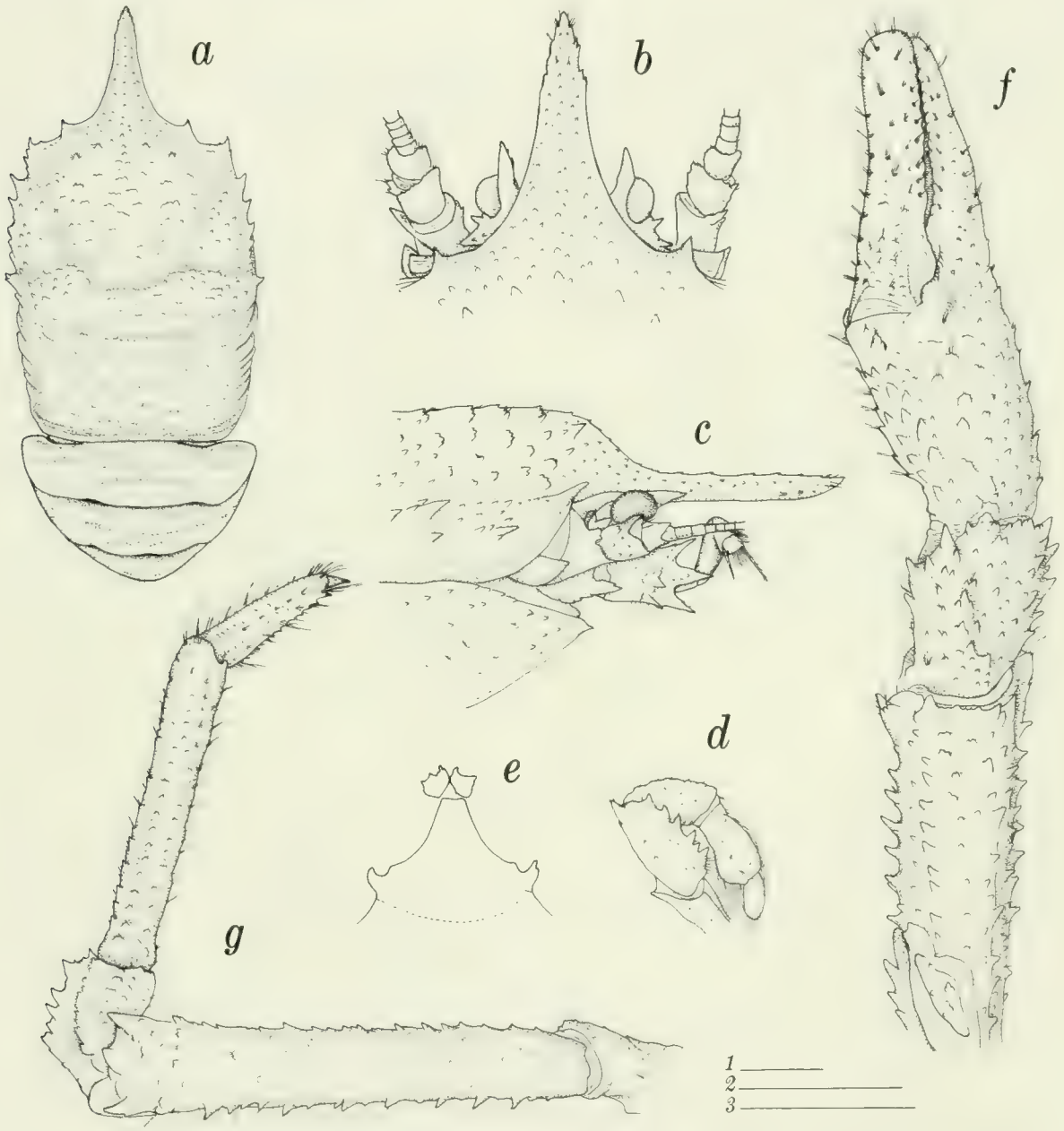

FIGURE 1.—*Munidopsis marianica*, holotype ♀: *a*, carapace, abdominal segments 2–4 in folded position, dorsal; *b*, parts of anterior carapace and associated appendages, dorsal; *c*, parts of anterior cephalothorax and associated appendages, lateral; *d*, merus of right third maxilliped with parts of adjacent articles; *e*, sternites at base of third maxillipeds and chelipeds; *f*, right cheliped; *g*, left first walking leg. Scales: 1(*a*), 2 (*b*, *c*, *f*), 3 (*d*, *e*, *g*) = 10 mm.

lateral margin; carpus spiny except on ventral surface; palm strongly spiny on mesial and lateral surfaces, less so dorsally but with scattered rugosities there as well; fingers about as long as palm, spooned, especially at tips, prehensile edges almost entire but imperceptibly crenulate, tips close fitting.

Walking legs rather long, first walking leg (Fig. 1*g*) reaching almost to tip of chela, second and third walking legs reaching almost to base of dactyl on preceding leg (right second walking leg missing from holotype); corresponding articles of respective legs approximately equal in length except for meri which decrease posteriorly; each merus with spiny dorsal crest ending in strong distal spine; prehensile surface with 2 rows of rugae, spines, and tubercles; carpi each with longitudinal dorsal and lateral rib, each ending in

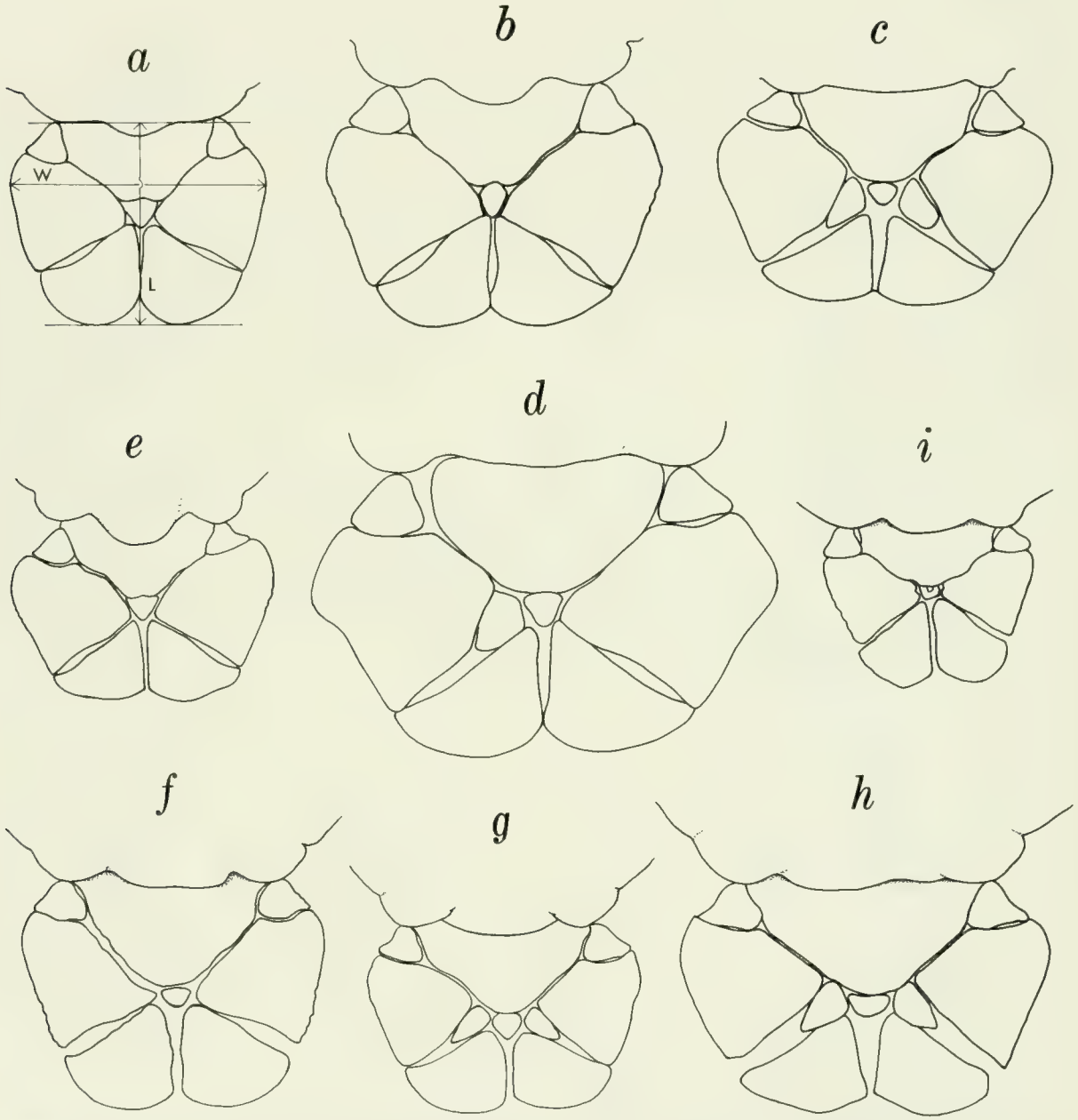

FIGURE 2.—Outlines of telson plates and distal margin of abdominal segment 6, lines on *a* indicate pattern for length (L) and width (W) measurements: *a*, *Munidopsis marianica*, paratype + USNM 240201; *b*, *M. tuftsi*, holotype ♂, USNM 171336; *c*, *M. subsquamosa*, syntype BM 88:33; *d*, *M. subsquamosa aculeata*, holotype ♂, BM 88:33; *e*, *M. crassa* holotype ♀, USNM 8536; *f*, *M. lignaria*, holotype ♂, USNM 240202; *g*, *M. ciliata*, ♀, USNM 151856, Celebes, Indonesia; *h*, *M. nitida*, ♂, USNM 150580, St. Croix Basin, Caribbean Sea, note atypically sinuous terminal margin on median lobe of segment 6; *i*, *M. granosicorium*, holotype ♀, USNM 240205.

well-developed terminal spine, and with secondary spine on distal margin between them, dorsal rib spiny, lateral rib less so; each propodus slender, with dorsal, dorsolateral, and lateral ridges spiny in proximal half but less so distally, dorsal spines pronounced; each dactyl slender, acute corneous tip preceded by row of 14 or more movable spines on prehensile edge. Chela on slender fifth leg with well-developed cleaning brush (chelae missing on holotype).

Eggs on holotype ♀ few, large, principal axes measuring 1.3 × 1.6 mm.

Remarks.—Observations televised during *Alvin* Dive 1845, 18°13′N, 144°42′E, 3,716 m, 6 May 1987, Pilot Hollis, Observers Ohta, Kono, included views of *Munidopsis* that may be this species.

Munidopsis marianica resembles a number of species in the genus that normally have epipods restricted to the first pereopods, eyespines extending beyond the cornea, and chelipeds lacking a denticulate carina on the distolateral margin of the chela, including *M. crassa* Smith, 1885; *M. similis* Smith, 1885; *M. subsquamosa* Henderson, 1885; *M. barnardi* Kensley, 1968; *M. tuftsi* Ambler, 1980; and *M. geyeri* Pequegnat and Pequegnat, 1970. *Munidopsis similis*, originally considered to be a variety (subspecies) of *M. crassa* (see Smith 1885:496), is different from this group in lacking epipods on all pereopods (Pequegnat and Pequegnat 1970:139). *Munidopsis geyeri* was synonymized with *M. subsquamosa* (see Ambler 1980:26), and *M. barnardi* from South Africa (Kensley 1968:290) will in all probability be merged with *M. subsquamosa* (unpubl. data). Therefore, the remaining three species are compared with the present new species.

The closest relative to this new species seems to be *M. tuftsi*, known from off Oregon (Ambler 1980:24). The shared characters are relatively long chelipeds, particularly meri that extend nearly to the rostral tip, the anterior half of the carapace that bears tubercles or spines rather than rugae, and the strongly convex posteromedian margin of the sixth abdominal segment that distinctly overreaches the lateral lobe on each side. However, *M. tuftsi* differs from *M. marianica*—the walking legs are more strongly spinose but the chelipeds are less spiny; the anterior half of the carapace, especially the anterior branchial region, bears distinct dorsal spines; the telson is relatively wide (length-width ratio, 0.71 in the holotype of *M. tuftsi*, 0.79 [$\bar{x}$] in *M. marianica*), the midlateral plate is more markedly convex on the distolateral margin; and the rostrum is distinctly carinate dorsally, relatively high and strongly upcurved. Most clearly different in the 2 species are dactyli of the walking legs (Fig. 3*b*, *c*); they terminate in a short corneous, curved spine. In *M. tuftsi*, the ultimate ventral tooth is distinctly closer to the tip of the terminal spine than to the penultimate

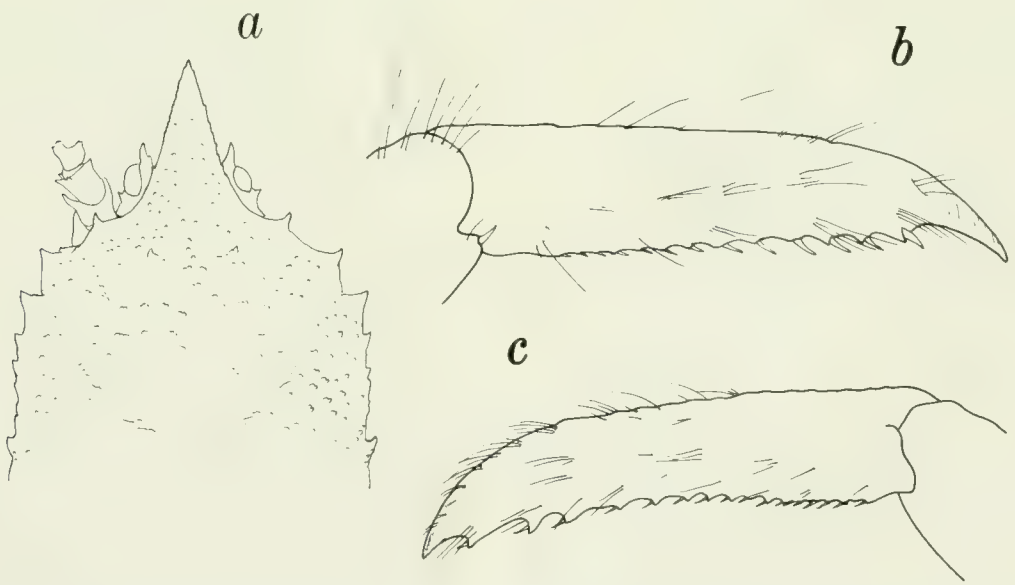

FIGURE 3.—*Munidopsis marianica*, paratype ♀, USNM 240201: *a*, anterior carapace with parts of appendages, dorsal; *b*, dactyl of first walking leg; *c*, *M. tuftsi*, holotype ♂, USNM 171336, dactyl of first walking leg.

ventral tooth, while in *M. marianica* the terminal spine is elongate and the ultimate ventral tooth is nearer to the penultimate one. The above listed differences were confirmed by examination of the holotype of *M. tuftsi* (USNM 171336) as well as an additional male specimen of *M. tuftsi* taken at *Galathea* station 450 in the Celebes Sea (unpubl. data).

Munidopsis subsquamosa and *M. crassa* are also similar to *M. marianica*. General characteristics of *M. subsquamosa* were examined on 2 snytypes (♂, and softened remains, BM 88:33; and the holotype ♂ of *M. subsquamosa aculeata*, BM 88:33), both described by Henderson (1885, 1888) now deposited in the British Museum (Natural History), and on 2 examples of *M. subsquamosa* taken rather near its type locality by the *Soyo Maru*, reported earlier by Baba (1982:114). Examined also were the abdominal fragment of the holotype of *M. crassa* (USNM 8536) in which both the telson and the sixth abdominal segment are intact, and 2 specimens (1 ♂, 1 ♀) referable to *M. crassa* (USNM 231328) that taken by the RV *Alvin* from the North Atlantic Ocean southeast of Massachusetts (lat. 38°18′24″N, long. 69°35′30″W, 3,506 m) very near the type locality. The anterior branchial region of the carapace usually bears elevated, scalelike striae in *M. subsquamosa* instead of tubercles or spinules as in *M. crassa* and *M. marianica*. The posteromedian margin of the sixth abdominal segment is feebly convex and never exceeds the end of the lateral lobes in *M. subsquamosa*, but it is markedly produced, overreaching the lateral lobes in *M. crassa* and *M. marianica*. The telson (Fig. 2*a–e*) is relatively narrower in *M. marianica* (length-width ratios: 0.61–0.65 in *M. subsquamosa*; 0.68–0.70 in *M. crassa*; 0.79 [$\bar{x}$] in *M. marianica*). The fingers of the cheliped are distally narrowed in *M. subsquamosa* and *M. crassa*, but uniformly wide throughtout the length so as to form a sharply defined ventral spoon in *M. marianica*. The merus of the cheliped in *M. subsquamosa* and *M. crassa* is middorsally ridged, more sharply so toward the proximal end, instead of being bluntly ridged as in *M. marianica*. The mesial eyespine is directed anterolaterad in *M. subsquamosa* and *M. crassa*, while in *M. marianica* it is directed nearly straight forward. The rostrum is straight and horizontal in *M. marianica*, but usually curving dorsad in *M. subsquamosa* and *M. crassa*. Finally, the merus of the third maxilliped is more spinose on the flexor margin in *M. marianica* (bearing about 6 spines) than in *M. crassa* and *M. subsquamosa* (3 or 4 spines).

Etymology.—Named for the type locality.

Munidopsis lignaria New Species

Figures 2*f*, 4

Munidopsis ciliata, Ambler, 1980:19, fig. 4.—not *M. ciliata* Wood-Mason *in* Wood-Mason and Alcock, 1891:200.

Munidopsis sp. Van Dover, 1988:6, unnumbered fig.

Material studied.—Eastern Pacific Ocean, Cascadia Basin off Oregon: USNM 240202. Holotype ♂. 44°39.8′N, 125°36.4′W, 2,875 m, RV *Yaquina* cruise Y 7001 B, stn CP-1-E, BMT 184, 16 March 1970, transferred from OSUBI 00188.—USNM 240203. Allotype ♀. 45°18.6′N, 126°31.5′W, 2,750 m, RV *Yaquina* cruise Y 7001 B, stn CP-2-C, BMT 265, 18 February 1971, transferred from OSUBI 01578.—OSUBI 00189. Paratypes, 19 ♂, 13 ♀. 44°53.7′N, 126°33.4′W, 2,774 m, RV *Yaquina*, cruise Y 7001 B, stn CP-2-D, from log collected in beam trawl 162, 19 January 1970.—USNM 171342. Paratype ♀. 45°55.3′N, 125°36.1′W, 2,030 m, RV *Yaquina* cruise Y 7003B, stn CP-1-A, BMT 194, 20 March 1970.—USNM 171343. 6 ♂, 7 ♀. 45°52.5′N, 126°40.8′W, RV *Yaquina* cruise Y 7001 B, stn CP-2-A, BMT 154, 16 January 1970.

East Pacific Rise off south central Mexico: USNM 240204. Paratypes, 8 ♂, 12 ♀. Western limb of overlapping spreading center near 11°52′N, 103°51′W, 2,750 m, *Alvin* Dive 2000, 22 March 1988, from a piece of wood measuring about 15 × 30 cm, Pilot Ralph Hollis, Observers W. Bryan and R. Hekinian (IFREMER). This material was donated to us by Cindy Van Dover, Woods Hole Oceanographic Institution, Woods Hole, MA.

Measurements in mm.—Holotype ♂, carapace length including rostrum 15.0, margin of orbit to posterior edge of carapace 10.2, maximum carapace width 9.0; Allotype ♀, same (respectively), 16.5, 11.6, 10.2; smallest Paratype ♂, USNM 240204, same 9.0, 6.7, 6.3; smallest Paratype ♀, USNM 240204, same, 9.2, 6.5, 5.5.

Description.—Carapace (Fig. 4*a–b*), exclusive of rostrum, longer than broad, moderately arched transversely; anterior and posterior

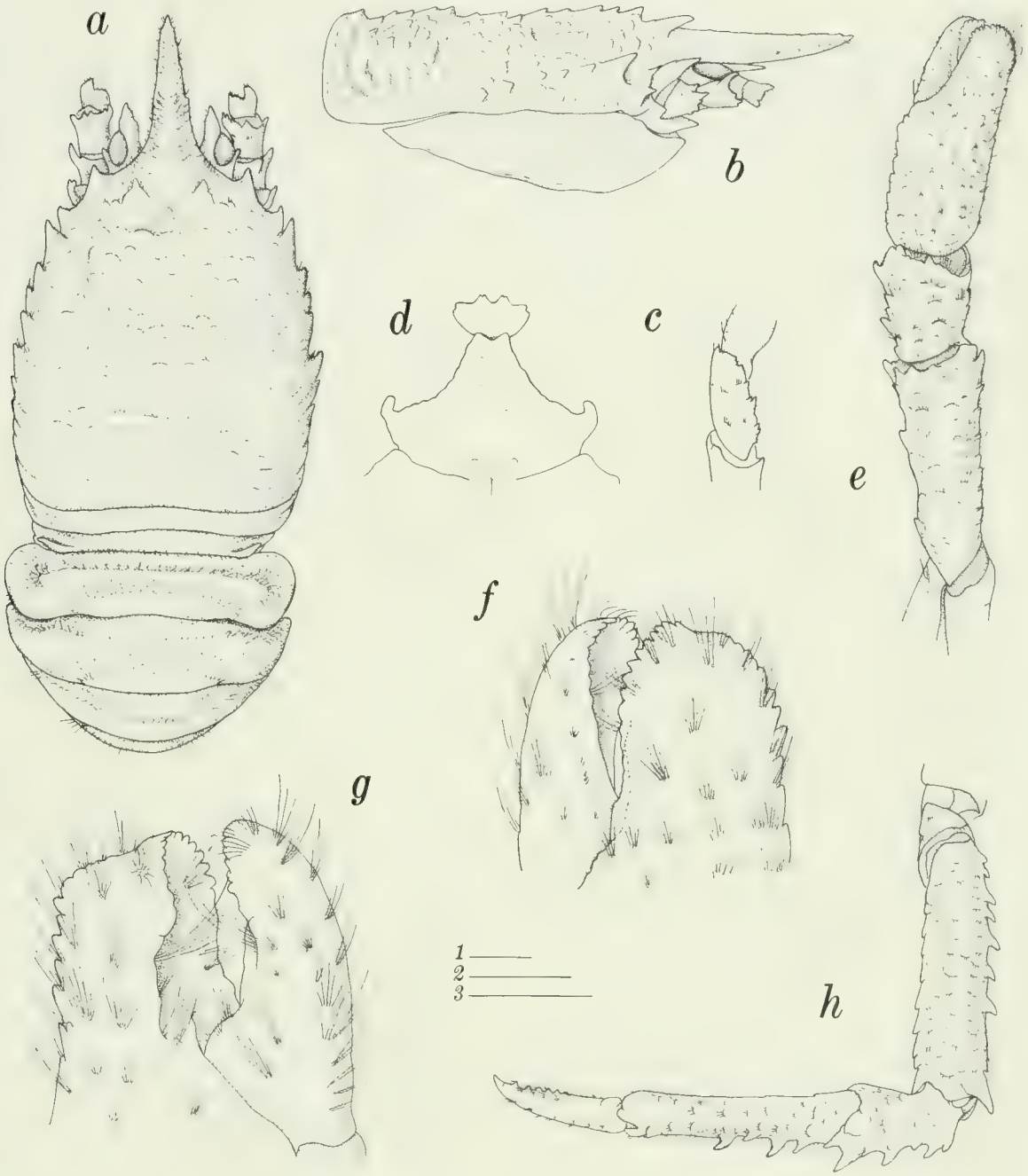

FIGURE 4.—*Munidopsis lignaria*, holotype ♂, USNM 240202: *a*, carapace and parts of anterior appendages, abdominal segments 2–4 in folded position, dorsal; *b*, cephalothorax and parts of anterior appendages, lateral; *c*, merus of right third maxilliped and parts of adjacent articles; *d*, sternites at base of maxillipeds and chelipeds; *e*, right cheliped, and views of fingers; *f*, dorsal; *g*, ventral. Scales: 1(*c*, *d*), 3(*f*, *g*) = 1 mm, 2(*a*, *b*, *e*, *h*) = 3 mm.

cervical grooves apparent, transverse depression in anterior part of cardiac region. Rostrum narrowly triangular, tip exceeding eyestalks by their own or slightly greater length; horizontal dorsal surface nearly smooth, with low but distinct carina becoming obsolescent between prominent gastric spines. Frontal margin with acuminate, slightly hooked antennal spine lateral to eyestalk followed by concavity ending in small, acute anterolateral angle. Gastric region bearing short setose rugosities arranged in more or less concentric arcs behind strong gastric spine at either side of midline (reduced secondary gastric spine lateral to each in large indi-

viduals). Anterior branchial region bearing less prominent ciliated rugosities, its lateral margin with strong anterior spine followed by 4 spines successively smaller in size. Posterior branchial region with moderately developed spine at anterolateral corner and more distinct and transversely developed setose rugae, with tendency in larger adults for these to be most elongate across anterior and central part of cardiac region. Shallowly concave posterior margin preceded by prominent raised, ciliated submarginal rim of nearly uniform width. Lateral plate obliquely rugose, projecting anteriorly below antennal peduncle, its rather rounded tip bearing minute spine.

Abdomen (Fig. 4*a*) unspined, but segments 2 and 3 boldly ridged transversely; ridging of segment 4 transitional; segments 5 and 6 smooth, latter with posterior margin trilobate, distal margin of lateral lobes convex, that of broader median lobe very shallowly concave. Telson (Fig. 2*f*) composed of 8 plates, length-width ratio in holotype 0.85, in smaller ♀ paratype 0.83, midlateral plate convex on distolateral margin.

Eyes (Figs. 4*a–b*) moderate in size; well exposed, smoothly ovate cornea cupped within broad-based slightly movable ocular peduncle extended into elongate mesiodorsal spine; spine horizontal or directed obliquely upward at low angle; peduncle ornamented with few setae and tiny irregular obsolescent spinules, much shorter mesioventral spine, and intermediate length lateral spine.

Basal article of antennular peduncle with crested dorsal margin minutely and irregularly serrate, extended into slender dorsolateral spine, broader lateral spine below, base of each flanked laterally by cluster of irregular, small, obsolescent spinules on inflated lateral side of article; mesial edge with crenulate scalloped margin. Antennal peduncle with fixed basal article extended into stout, flat, ventral spine and shorter lateral spine with crenulate margin; succeeding articles short, second bearing slender lateral angle, third with scalloped and crenulate distal margin, fourth with scalloped distal margin, its dorsolateral projection stoutly spinelike.

Third maxilliped with ischium shorter than merus; bearing mesial crest armed with finely uniform, evenly spaced corneous-tipped spines; anteroventral angle acute. Basis with 2 low spines in line with crest on ischium. Merus (Fig. 4*c*) with few obsolescent spines preceding 3 principal spines on flexor margin, proximal and middle spines incompletely doubled; extensor margin broadly arched, strong, acute spine at anterodistal corner. Carpus, propodus, and dactyl folded on merus-ischium and about as long as those 2 articles together, dense setation on dorsal surface of each, and distally on flexor surface of propodus and dactyl. Sternite at base of third maxilliped (Fig. 4*d*) with crenulate anterior margin on angular mesial and lateral lobes.

Epipod present on first pereopods (chelipeds).

Chelipeds (Fig. 4*e–g*) stout, subequal, ornamented with moderately developed, variably setose rugosities tending to arrangement in longitudinal tracts; ischium with short lateral spine and mesial ridge bearing obsolescent subterminal spines; merus bearing 3 principal mesial spines, 1 distodorsal spine, and distoventral spine on mesial and lateral margins; carpus with dorsolateral row of tubercles and mesiodorsal row of 3 spines; palm nearly smooth, few obsolescent tubercles on dorsomesial surface; stout fingers shorter than palm, spooned at tips, prehensile edges close fitting, crenulate; crest of small spines at distolateral angle of fixed finger.

Walking legs rather long, first walking leg (Fig. 4*h*) exceeding tip of chela, second and third reaching to near base of dactyl on preceding leg; corresponding articles of respective legs approximately equal in length except for meri which successively decrease posteriorly; each merus with crest on dorsal margin ending in distal spine, and corresponding crest on ventrolateral margin; carpi with longitudinal spiny dorsal and tuberculate dorsolateral crest, each ending in more or less well-developed spine; each propodus slender, bearing crests in line with those of carpus, dorsal crest bearing 2 remote spines in proximal half, each with small movable spine distolaterally at base of dactyl, another sometimes preceding it in distal ⅓ of length, and smaller movable spine at distomesial corner; each dactyl slender, acute corneous tip preceded by row of 10–12 movable spines on flexor margin. Slender, chelate fifth leg with well-developed cleaning brush on palm and somewhat pointed but flattened dactyl opposed by similar setae on distal end of propodus.

Variation.—There is minor variation in ornamentation of the specimens available for study, large adults being relatively more coarsely ornamented than smaller individuals.

Remarks.—*Munidopsis lignaria* is allied to *M. ciliata* Wood-Mason of the western Indo-Pacific,

M. nitida (A. Milne-Edwards, 1880) of the western Atlantic, and more distantly, *M. verrilli* Benedict, 1902 of the eastern Pacific. Ambler (1980:19) correctly differentiated, from *M. ciliata*, the new species with "shorter, stouter spines on the carapace and legs; shorter setae covering the carapace and legs; rostrum with a narrower base; and no extra spine between the anterolateral and antennal spines, as sometimes occurs in the *Albatross* specimens." However, she regarded the differences between these 2 forms as racial or varietal rather than specific, a view paralleling that of Faxon (1895:84), who identified eastern Pacific specimens collected by the *Albatross* as *M. ciliata*, and stated that differences between *M. nitida* and *M. ciliata* "appear to be of racial or varietal, rather than specific, value." However, he reserved judgment until the distribution of each might become better known. It does appear that the specimens seen by Faxon closely resemble *M. ciliata*, although only those from *Albatross* stations 3392 and 3393 are now present in the MCZ crustacean collection, and there is no record of specimens from stations 3353 and 3363 in the MCZ crustacean catalog[3]. There are minor differences in spination of the walking legs of *M. ciliata* and those of the available specimens seen by Faxon, but before deciding the status of this eastern Pacific material a search for the missing material should be made.

Munidopsis ciliata reaches noticeably larger size as an adult than does *M. lignaria*. *Munidopsis ciliata* is characterized by much longer and more slender spination, and much longer and more prominent setae springing from rugosities of the carapace and legs than on *M. lignaria*.

Munidopsis nitida has well-developed acute spines on legs and cephalothorax, but rugae are far less prominent than in either *M. ciliata* or *M. lignaria*, and unlike either of these has the rostrum upturned distally at a low angle.

Munidopsis ciliata, *M. lignaria*, and *M. nitida* have a distally trilobate margin on the sixth abdominal segment (Fig. 2*f–h*), each with a convex lobe to either side and a broader median lobe; the middle portion of the median lobe of *M. lignaria* usually has a very shallowly concave distal margin, that of *M. ciliata* is slightly convex and slightly arched dorsally, and that of *M. nitida* is almost transversely straight except for a slight concavity at either side where it joins the respective lateral lobes. *Munidopsis lignaria* has 8 plates in the telson (Fig. 2*f*) whereas the other species have 10. The telson of *M. lignaria* has a length-width ratio of 0.85 in the holotype, and 0.83 in a much smaller paratype; that ratio in *M. ciliata* is 0.70, and in *M. nitida* it is 0.72.

The chelae of these 3 species are similar, having close fitting, crenulate distal edges on the tips of the spooned fingers, and a serrate distolateral angle on the fixed finger. Width-length ratios of the chelae are 0.50 in *M. lignaria* and *M. ciliata*, and 0.41 in *M. nitida*. Both *M. lignaria* and *M. nitida* have been collected in association with wood (see material studied; Williams and Turner 1986), and Van Dover (1988) found numerous wood fragments in the stomachs of *M. lignaria* collected off Mexico. The chelae of the latter 2 species look as if they could be used for boring, tunneling in, or shredding wood. There are no published habitat data for *M. ciliata*. However, Wolff (1979) recorded the association of *M. vicina* Faxon, 1895, *M. hendersoniana* Faxon, 1895, and *Munidopsis* sp. with wood. The first two of these species, having chelae similar to those discussed here (see Faxon 1895: pl. XVIII, fig. 2*a* and pl. XXIV, figs. 2, 2*c*) were listed as utilizing wood for food, and the third sheltering in it.

Munidopsis verrilli, with which Ambler (1980) also compared the new species, is much more distant, being a larger species with conspicuously setose legs, relatively longer and stronger chelipeds lacking epipods, more coarsely ornamented cephalothorax with rugosities in a different pattern on both carapace and side plates, a relatively shorter rostrum, and more globose eyes from the margin of which the 3 spines project prominently at divergent angles, to mention the most obvious differences.

Etymology.—From the Latin "lignarius", of or belonging to wood, for the association of the species with pieces of wood.

Munidopsus granosicorium New Species

Figures 2*i*, 5

Material studied.—USNM 240205. Holotype ♀ (ovig.), eastern Pacific Ocean off Strait of Juan de Fuca, 48°38.7′N, 126°57.6′W, 2,020 m, RV *Destiger*, DWD-BMT 10, 11 September 1971.

Measurements in mm.—Carapace length including rostrum 9.7, margin of orbit to posterior

[3]Ardis B. Johnston, Harvard University Museum of Comparative Zoology, Cambridge, MA 02138, pers. commun. October 1988.

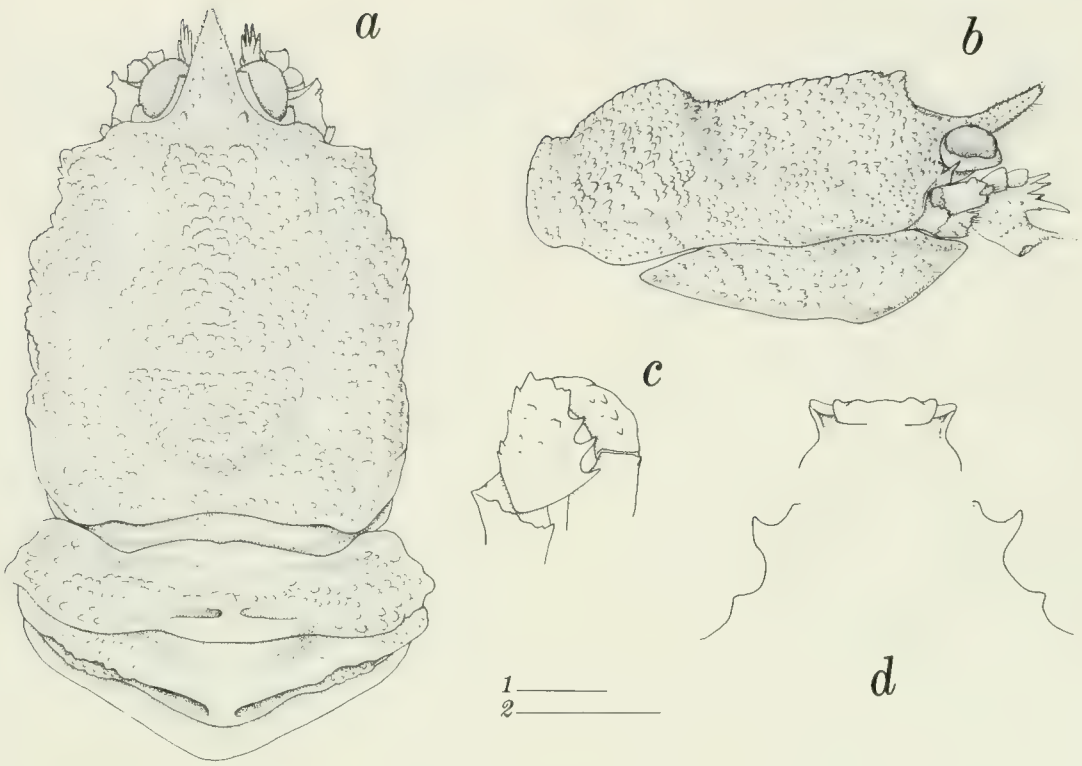

FIGURE 5.—*Munidopsis granosicorium*, holotype ♀, USNM 240205: *a*, carapace and parts of anterior appendages, abdominal segments 2–4 in folded position, dorsal; *b*, cephalothorax and parts of anterior appendages, lateral; *c*, merus of right third maxilliped and parts of adjacent articles; *d*, sternites at base of maxillipeds and chelipeds. Scales: 1(*c*, *d*) = 1 mm, 2(*a*, *b*) = 3 mm.

edge of carapace 7.4, maximum carapace width 7.7

Description.—Integument iridescent. Carapace (Fig. 5*a*, *b*), exclusive of rostrum approximately as long in midline as broad, sculptured, variably ridged longitudinally; anterior and posterior cervical grooves apparent but obscure, prominent transverse ridge across anterior part of raised cardiac region; crowded rugae on dorsal surface moderately elevated, most closely clustered and transversely elongated on median prominences, especially on cardiac region, giving an overall uneven, variably pebbled appearance; a nearly smooth and slightly concave spot to either side of midline at anterolateral corner of cardiac region. Rostrum broadly subtriangular, transversely arched, base broader than midsagittal length; dorsal surface in lateral view with concave base smoothly curving into upwardly inclined distal part having almost straight dorsal margin, apparently acute tip slightly blunted by damage; lateral margins anterior to eyes serrate, but concave posterior margins adjacent to eyes nearly smooth; scattered tubercles on anterior 5/8 of length much smaller and more numerous than larger, symmetrically arranged rugae on posterior 3/8; anterior part with noticeable brush of plumose setae, densest ventrally. Sinuous frontal margin with broad angle lateral to eyestalk continued laterad as thin raised edge curving into a small serrate lobe proximolateral to basal article of antenna; anterolateral angle densely and sharply rugose, followed by similar but somewhat more broadly projecting lateral margin of anterior branchial region, margin thinner on posterior branchial region. Posterior margin broadly and shallowly concave, slightly sinuous; preceded in turn by submarginal narrow rugose ridge, and transverse narrow smooth tract. Lateral plate projecting anteriorly below antennal peduncle, its rather angular anterior tip bearing minute spine in line with base of eye; strongly rugose posterior part separated from somewhat less strongly rugose anterior part surrounded by impressed groove running submarginal to anteroventral aspect, then sweeping posterodorsally and recurving

anteriorly below line of rugae bordering lateral suture to point behind anterior tip.

Abdomen (Fig. 5*a*) unarmed but deeply sculptured; transverse ridges of segments 2–4 lightly rugose centrally but more strongly so laterally; segments 5 and 6 punctate, lightly rugose laterally. Telson (Fig. 2*i*) composed of 8 plates, length-width ratio 0.85, midlateral plates slightly convex on proximolateral margin.

Eyes (Figs. 5*a–b*) prominent; well exposed; smoothly ovate cornea cupped within broad based, fixed ocular peduncle bearing small anteromesial rugose patch but no spine; small, subtriangular plate posterolaterally adjacent to eye and anterior to frontal margin.

Basal article of antennular peduncle with distal margin irregularly crenulate; crest of slender compound dorsolateral spines and stronger anterolateral spine flanked by inflated lateral surface with irregular, small spinules at periphery; mesiodistal spine obsolescent. Antennal peduncle with fixed basal article extended into fimbriate distal margin, flat ventral spine, and shorter crenulate lateral spine; succeeding articles short, second bearing stout compound lateral angle and small, simple, distomesial angle; third with acute mesiodorsal angle; fourth with scalloped distal margin.

Third maxilliped with ischium shorter than merus, bearing mesial crest armed with finely uniform, evenly spaced corneous tipped spines, an acute distodorsal angle, and subrectangular distoventral angle flanked laterally by obsolescent spine. Basis with 0 or 1 obsolescent spine in line with crest on ischium. Merus (Fig. 5*c*) with 3 strong spines on flexor margin; distal margin irregular; extensor margin broadly arched, bearing 4 obsolescent spines and a more prominent spine distally; ventral surface lightly rugose. Carpus, propodus, and dactyl folded on merus-ischium and about as long as those 2 articles together; dense setation on dorsal surface of each, and distally on flexor surface of propodus and dactyl. Sternite at base of third maxilliped (Fig. 5*d*) rather slender, anterior margin bilobed, mesial lobe surmounted by small spine.

Epipods present on coxae of pereopods 1–3. Pereopods missing.

Eggs few, large, principal axes measuring 1.3 × 1.9 mm.

Remarks.—The distinctiveness of *Munidopsis granosicorium* leads us to describe it as a new species even though it is represented by a single imperfect specimen. This species seems close to *M. follirostris* Khodkina, 1973, from off the Pacific coast of South America (30°13′9″S, 78°47′W, 1,280 m) in general features of the carapace, the abdomen and telson, and in the relatively large cornea; however, it differs in having the rostrum triangular rather than markedly constricted near the base, and the gastric region elevated in anterior profile rather than evenly rounded (see Khodkina 1973).

More distantly, presence of epipods on the chelipeds and first two ambulatory legs links the species to *M. rostrata* (A. Milne Edwards, 1880) and *M. spinosa* (A. Milne-Edwards, 1880), but lack of any spine on the gastric region of the carapace separates it from these 2 species. The rostrum also differs from that of *M. rostrata* in lacking distinct lateral teeth, and from that of *M. spinosa* in having some very small marginal spines or tubercles (see Chace 1942). The short, immovable, spineless eyestalks link the new species to *M. espinis* Benedict, 1902, but it differs from that species in the deeper sculpturing of the carapace and abdomen, and in the dense scattering of small rugae but lack of spines on the carapace, and in having the merus of the third maxilliped armed with 3 rather than 2 spines on the flexor surface. There is only one record of *M. spinosa* from the western Pacific, and *M. rostrata* is represented by records from a circumglobal band between lat. 40°N and 35°S (see Baba 1988).

Etymology.—The specific name is a noun in apposition from the Latin, "granosus", full of grains, and "corium", leather, for the pebble-grained surface of the carapace resembling Scotch grained leather.

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Catch Efficiencies of Purse and Beach Seines in Ivory Coast Lagoons

Emmanuel Charles-Dominique

ABSTRACT: Catch efficiencies of two commonly used fishing gears in Ivory Coast lagoons, purse seine and beach seine, were studied. Only fish larger than the 100% mesh retention size (L_{100}) were considered. Escapement was estimated from the retention rates of marked fish released within the closed seines in shallow waters. Simple and reliable upper estimates of the catch efficiency were provided by these retention rates, which ranged from 10% to 79% for the purse seine and from 35% to 53% for the beach seine depending on the species. The purse seine efficiency was estimated by performing 25 sets (one set covering 0.72 ha) inside the closed beach seine (covering 9.4 ha), on both marked and unmarked populations of the bagrid *Chrysichthys* spp. and the cichlid *Tilapia guineensis*. The efficiency was close to 15% for the species considered, but this estimate may be sensitive to experimental bias (marking and "enclosure" effects). Avoidance, calculated for the purse seine from escapement and efficiency, appears to be considerable. Comparison of the catch rates by the two gears showed interspecies selectivity ("species selectivity") and intraspecies selectivity ("size-selectivity", regardless of mesh size). An understanding of both types of selectivity appears to be essential for an interpretation of the catch rates.

Artisanal fisheries are well developed in Ivory Coast lagoons, yielding from 10,000 to 20,000 tons of commercially valuable fish per year. Various stock assessment programs have been initiated at the Abidjan C.R.O. (Centre de Recherches Océanographiques) for fisheries management purposes during the last few years, but more direct methods of estimating fish abundance from catch rates are needed. The catch rates, which can be considered as relative abundance indices, can be converted into absolute abundance measurements, if the efficiency of fishing gear is known or can be estimated (Beverton and Holt 1956). Unfortunately, this is always a difficult process because efficiency depends upon various factors such as the behavior of fish, the environmental conditions (depth, nature of the bottom, etc.), and the physical characteristics of each particular gear. Previous studies have mostly dealt with towed gears such as trawls and plankton nets (Barkley 1972; Kjelson and Colby 1977; Merdinyan et al. 1979). The efficiency of these gears appeared to be a function of the active avoidance rate by fish, and models can be designed to explain, at least partially, the process (Barkley 1964). Measures of gear efficiency have been based on the "swept-area method" (Beverton and Holt 1956). Mark-recapture experiments have been made in well-defined areas, and the recapture rate has been compared with the ratio between the area swept by the gear and the area where the marked fish have been distributed (Kuipers 1975; Loesch et al. 1976; Watson 1976; Kjelson and Johnson 1978). Unlike trawl nets, surrounding nets and beach seines have rarely been studied in terms of efficiency, except the Danish seine (Hemmings 1973), which can be compared with a beach seine. For the surrounding–type gears, there are two different phases: 1) the shooting of the net, during which active avoidance takes place, and 2) the hauling of the net on board once the circle is closed, during which escapement can occur.

In this report, an experiment, based on an estimation of catchability according to the areas swept by the gears, in conjunction with a mark-recapture procedure, is described. This study was designed to better understanding multi-species catch-rates and to provide estimations of catchability for stock assessment.

MATERIAL AND METHODS

The two main fishing methods used in the Ivory Coast lagoons are the beach seine without a bag for shallow waters (about 1,200 m long) and the purse seine for depths of 2 m or more (ranging from 300 to 500 m long). Both gears reach the bottom and catch pelagic species as

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well as demersal species (Durand et al. 1978; Charles-Dominique 1983).

In this experiment, the purse seine was 305 m long on the lead-line and 14 m deep; the net was in excellent condition. The beach seine was 1,100 m long and 8 m deep; although the net was carefully checked, a few holes may have been overlooked owing to its very large size. The mesh size for both seines was 14 mm (bar measure).

Catchability (q) is the probability of capturing one fish from the standing stock by one unit of effort ($q = C/N$, where C is the catch in number per unit of effort and N the total standing stock). It may be divided into three elements (Laurec and Le Guen 1981): 1) overall accessibility (p_A), the probability of the presence of one fish in the fishing area A; 2) local accessibility (p_a), the probability of the presence of one fish in the area a that has been swept by the gear in one fishing operation; and 3) efficiency (e), the ratio of the number of fish caught to the number of vulnerable fish that were present in the area swept in one set (see Figure 1). Thus,

$$q = p_A \cdot p_a \cdot e \tag{1}$$

In shallow waters, where the net reaches the bottom, the efficiency can be broken down into a product of three retention rates, corresponding to three successive phases: 1) avoidance (u), beginning with the net-shooting and ending with its closing; 2) escapement through the mesh (v), occurring if the fish size is less than L_{100} (the size at which 100% of fish are retained by the mesh); and 3) other forms of escapement (w), i.e., jumping over the net, burrowing or slipping through holes in the net or under the lead-line.

This catch efficiency can be written as follows:

$$e = u \cdot v \cdot w \text{ (purse seine)} \tag{2}$$

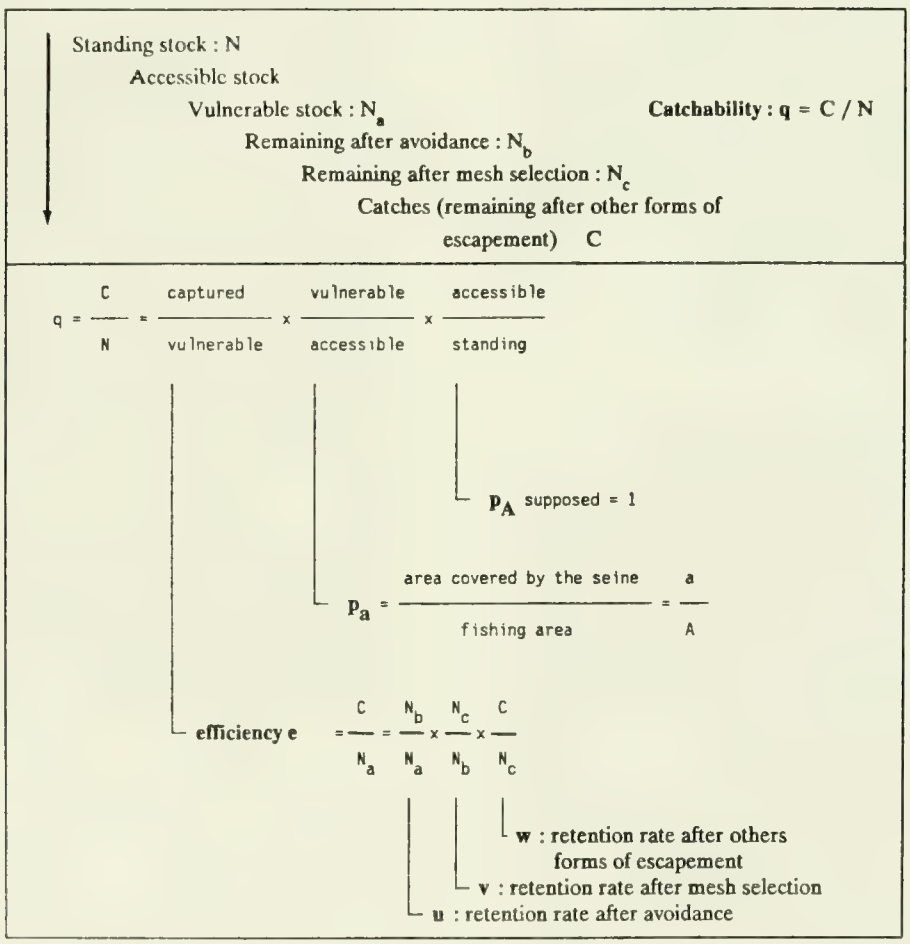

FIGURE 1.—Schematic representation of the catchability parameters for a seine in shallow waters and the catchability equation that comprises these parameters.

$$E = U \cdot V \cdot W \text{ (beach seine)} \qquad (3)$$

where capital letters refer to the beach seine and small letters to the purse seine (Table 1).

TABLE 1.—Summary of the methods used in this paper to estimate the parameters of the catchability, as defined in the text and on figure 1. Small letters refer to the purse seine and capital letters to the beach seine.

Parameters	Purse	Beach sine
Retention rate after escapement through mesh	v = for fishes greater than L_{100}, 100% mesh retention size	V = 1 (idem)
Retention rate after other forms of escapement	w = 15 independent mark-recapture estimates	W = 2 measures (W_1, W_2), 5 replica
Catchability	g = 5 measures using two methods (from captures and from recaptures)	—
Efficiency	$e = q \cdot a/A$ a = area covered by the purse seine (0.72 ha) A = area covered by the beach seine (9.4 ha)	E = W
Avoidance	$u = e/w$	supposed negligible

Two independent experiments were designed 1) to estimate the purse seine retention rate and 2) to estimate both the beach seine retention rate and the purse seine efficiency.

To estimate the purse seine retention rate, 15 mark-recapture experiments ($i = 1 \ldots 15$) were conducted in the open lagoon.[1]

Marking was done without anaesthetic by clipping either the superior lobe of the caudal fin, the right or left pelvic fin, or the adipose fin. Fish were stored in 1 m^3 floating cages with up to 100 fish per cage. The minimum size of the marked fish (mm) was greater than the L_{100}.[2]

At each experiment i, m_i fish were marked and released within the "closed" purse seine (i.e., when the two ends of the seine are joined together before pursing). At the end of the fishing operation, the species and sizes of the recaptured fish (r_i) were noted, and the retention rate ($w_i = r_i/m_i$) was calculated for each set. The weighted average (w) and variance ($v(w)$) were then calculated (Table 2).

$$w = \frac{\Sigma r_i}{\Sigma m_i}$$

[1]The experience was conducted in the Aby lagoon, one of the largest lagoons of the Ivory Coast (424 km^2), situated on the southwest of the country.

[2]Fish were larger than 9 cm (*Chrysichthys* spp.) or 10 cm (*Tilapia guineensis*). See footnote 3: Cantrelle et. al. (1983).

TABLE 2.—Estimation of the purse seine retention rate (w) from releasing m fish within the closed purse seine and recapturing them (r). C.V. is the coefficient of variation in percentage.

Species		Purse seine mark-recapture experiments															w	C.V.
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15		
Tilapia guineensis	*m*	20	3	12	15	2	34	45	1	18	23	9	16	5	28	21	0.544	27
	r	11	2	10	9	1	16	17	1	10	12	8	10	5	12	13		
Chrysichthys auratus	*m*	1	1		6		6	2	30		14	20	13	2	3	23	0.711	34
	r	0	0		6		3	1	29		9	13	11	2	3	9		
Chrysichthys maurus	*m*	19	40		26	25	27	41	62	14	67	2	7	32	5	38	0.760	21
	r	13	37		19	13	24	38	30	8	57	2	6	24	5	32		
Chrysichthys nigrodigitatus	*m*	2			18	8	1	10					2			2	0.581	33
	r	1			11	6	1	3					1			2		
Hemichromis fasciatus	*m*	1	3	2						9	2	2	1	17	6	4	0.787	32
	r	1	2	2						5	2	2	1	17	4	1		
Tylochromis jentinki	*m*					6		1	1	3		1	1			4	0.471	73
	r					3		0	0	0		1	1			3		
Gerres spp.	*m*											6	51	35	41		0.699	25
	r											4	47	19	23			
Callinectes amnicola	*m*				6	4	13	6	6	9	4	10	8		5		0.099	95
	r				1	1	2	1	1	0	1	0	0		0			

$$v(w) = \frac{\Sigma(r_i^2/m_i)}{\Sigma m_i} - \left[\frac{\Sigma r_i}{\Sigma m_i}\right]^2$$

In the second experiment, the beach seine was set in a shallow area of a lagoon where the average depth was 3 m. Fish were marked with a type-1 mark (M_1 fish) at the beginning of the experiment and released into the closed beach seine. A 30 min delay allowed the fish to disperse in the enclosure. Five successive purse seine sets were made randomly within the beach seine. Each set lasted about 22 minutes (the net was closed after about 3 minutes; the rings were placed on-board after about 9 minutes).

Species and size of captures and recaptures were recorded for each purse seine set; the unmarked fish were marked with a type-2 mark and stored in the floating cages. After the fifth purse seine set, the marked fish in good condition were released (M_2 fish). The retrieval of the beach seine took 6 hours. Species and size of the captures and recaptures (both M_1 and M_2 types) were recorded (Table 3). The experiment was repeated five times.

In this experiment, one should note that the storing period differed for marked fish: the marked-1 fish, captured the day before, were held captive approximately 15 hours, while the marked-2 fish on average were retained only 1 hour in the cages. Based on an aerial observation, the shapes of the seines were almost circular, although the beach seine was in some cases distorted by tidal currents; however, it was assumed that the nets were perfect circles (purse seine area 0.72 ha, beach seine area 9.4 ha).

Two retention rates by the beach seine (W_1 and W_2) were calculated for the whole experiment:

$$W_1 = R_1(M_1 - (r_{11} + r_{12} + r_{13} + r_{14} + r_{15}))$$

and for the second period of the experiment (beginning after the fifth purse seine set):

$$W_2 = R_2/M_2.$$

W_2 and W_2 correspond to fish that have stayed an average of 8½ hours and 6 hours in the enclosure respectively; thus, W_1 was expected to be lower than or equal to W_2. The difference between W_1 and W_2 was tested with a χ^2 test at the 0.05 level (Dagnélie 1975, p. 88). If W_1 and W_2 did not differ significantly, escapement was assumed not to have occurred during the purse seine fishing period. The mean retention rate (W) was calculated:

$$W = (R_1 + R_2)/(M_1 - (r_{11} + r_{12} + r_{13} + r_{14} + r_{15}) + M_2).$$

Assuming that the fish were equally available inside the enclosure, the overall accessibility (p_A) is 1 and the expectancy of the local accessibility (p_a) is equal to the ratio of the areas cov-

TABLE 3.—Experimental scheme used to measure the purse seine efficiency and the beach seine retention rate: a large beach seine reaching the bottom is set and closed over a shallow area, making a circular enclosure. M_1 fishes are marked and released within it at time 0, and a 30 min delay allows them to disperse. Five purse seine sets are then successively made within the enclosure. At every set i, the catches c_i and recaptures r_{1i} are recorded. The standing stock within the enclosure before set i is noted N_i. The unmarked fishes caught with the purse seine are marked with a type-2 mark (m_{2i}) and stored, then are released together after the fifth purse seine set (M_2). The beach seine is then retrieved and catches (C) and recaptures of both type-1 (M_1) and type-2 (M_2) are recorded.

Operations		Beach seine closed	Five purse seine sets (in hours elapsed) 0.5	1	1.5	2	2.5	Beach seine retrieved	Beach seine catches
Standing stock			N_1	N_2	N_3	N_4	N_5	N_6	
Releasing	mark-1	M_1							
Captures			c_1	c_2	c_3	c_4	c_5		C
Recaptures	mark-1		r_{11}	r_{12}	r_{13}	r_{14}	r_{15}		R_1
Marking	mark-2		m_{21}	m_{22}	m_{23}	m_{24}	m_{25}		
Releasing	mark-2							M_2	
Recaptures	mark-2								R_2

ered by the gears, $p_a = a/A$; therefore, according to Equation (1), $e = q \cdot A/a$.

Catchability q was estimated by using two partially independent methods (see notations on Table 1). In the first method (estimation "from captures"), catchability was estimated for each purse seining operation by the equation: $q_i = c_i/N_i$ ($i = 1...5$), where c_i represents captures at set i and N_i, the standing stock in the enclosure just before set i. When escapement did not occur during the first period ($W_1 = W_2$), the standing stock after last purse seine set (N_6) was estimated by the ratio of the beach seine captures (C) to the retention rate W. The previous values of N_i were then calculated backward ($N_i = N_{i=1} + c_i$, $i = 5...1$), and the q_i values follow.

In the second method (estimation "from recaptures"), catchability was estimated from the recaptures of marked-1 fish only when escapement did not occur during the first period ($W_1 = W_2$). In this case, $q_i = r_{1i}/M_{1i}$, where M_{1i} is the standing stock of marked-1 fish just before the set i. M_{1i} was calculated by successive subtraction of type-1 recaptures ($M_{1,i1} = M_{1i} = r_{1i}$).

The two methods of measuring q were compared using a distribution-free test (Wilcoxon's signed rank test, see Dagnélie 1975), which applies to paired data samples. The experimental design described above is summarized in Table 3.

Both methods rely on some underlying assumptions: A) no mortality of marked fish occurs; B) marked and unmarked fish have the same probability of escaping from the enclosure; C) the efficiency of the purse seine is equal for marked and unmarked fish; and D) all fish present in the enclosure have an equal probability of being caught. The method from captures relies on assumptions A), C), and D); the method from recaptures relies on A), B), and D).

RESULTS

Tagging and Holding Tolerance

No mortality of marked fish was observed during our experiment. This included the holding period in the floating cages as well as the fishing period (no dead marked fish were recovered in the seines). During the preliminary tests, however, marked fish of less robust species (*Ethmalosa fimbriata* and *Eucinostomus melanopterus*) were found dead in both the cages and the fishing nets.

Retention Rates

Purse seine captures and recaptures observed in the 15 independent mark-recapture experiments are listed in Table 2. The mean retention rates and the coefficient of variation were calculated for seven fish species and for the portunid crab *Callinectes amnicola*. The retention rate ranged from 0.47 to 0.79 for fish and was 0.10 for *C. amnicola*, which escaped in large numbers probably by burying itself. No fish were observed jumping over the purse seine net. Therefore, escapement appeared to be due to fish going under the lead-line.

Retention rates were estimated by size group for the two principal species, *Tilapia guineensis* and *Chrysichthys* spp. (grouping the three species, *C. maurus*, *C. auratus*, and *C. nigrodigitatus*). No difference was found between the size groups using a one-way analysis of variance by ranks (Kruskall-Wallis test, see Table 5).

The beach seine retention rates, W_1 and W_2, were calculated and their equality tested for the two principal species listed above (Table 4). For *Chrysichthys* spp., W_1 was always less than or equal to W_2. The mean retention rate (W) was 0.53. No size effect was found in the analysis of variance by size group (Table 5).

For *T. guineensis*, W_1 was less than or equal to W_2 in only two experiments. The mean retention rate was 0.35. In the three other experiments, the unexpected result of W_1 being greater than W_2 was found. This point will be discussed later. Again, no size effect was noticed (Table 5).

TABLE 4.—Estimation of the beach seine retention rates W_1 and W_2 (number of recaptured over number of released fish). If W_1 and W_2 do not differ significantly in one experiment (χ^2 test for the difference of two proportions, $P = 0.05$), the mean value W is then calculated. Parentheses mean a departure from the limit of application conditions of the test.

Retention rates	Capture dates (Oct. 1984)					
	8	9	12	13	16	Mean
Chrysichthys spp.						
W_1	7/15	57/78	28/107	78/141	31/106	
W_2	21/36	9/13	16/27	17/27	3/11	
χ^2	0.58	(0.36)	11.5	0.41	(0.13)	
W	0.55	0.73		0.57	0.29	0.53
Tilapia guineensis						
W_1	45/102	24/50	19/26	19/27	14/53	
W_2	38/90	28/92	27/102	13/36	8/27	
χ^2	0.07	4.31	19.5	7.2	0.09	
W	0.43				0.28	0.35

TABLE 5.—Comparison of the retention rates of purse seine (W) and beach seine (W_1 and W_2), calculated by size group: one-way analysis of variance by ranks (Kruskall-Wallis test). Critical value of $\chi^2_{0.95}$ is 7.81. M = mean, C.V. = coefficient of variation.

Purse seine					
Chrysichthys spp.					
Size	10–12 cm	13–15 cm	16–18 cm	>19 cm	χ^2_{obs}
W: M	0.725	0.776	0.686	0.622	2.21
C.V.	17	19	36	38	
Tilapia guineensis					
Size	8–11 cm	12–15 cm	16–19 cm	>20 cm	χ^2_{obs}
W: M	0.506	0.495	0.488	0.483	0.48
C.V.	50	43	68	49	
Beach seine					
Chrysichthys spp.					
Size	10–12 cm	13–15 cm	16–18 cm	>19 cm	χ^2_{obs}
W_1: M	0.563	0.476	0.386	0.377	0.75
C.V.	35	43	41	34	
W_2: M	0.565	0.632	0.600	0.250	0.40
C.V.	25	17	37	58	
Tilapia guineensis					
Size	8–11 cm	12–15 cm	16–19 cm	>20 cm	χ^2_{obs}
W_1: M	0.596	0.432	0.511	0.400	0.48
C.V.	35	23	66	47	
W_2: M	0.356	0.295	0.316	0.375	5.99
C.V.	38	25	67	111	

Catchability and Efficiency of the Purse Seine

The catchability equivalent to a purse seine set was estimated using both methods from captures (Table 6) and recaptures (Table 7). The mean and the standard deviation were then calculated.

For *Chrysichthys* spp., using the method from captures, q_c equaled 2.35% (SD = 5.38), and using the method from recaptures, q_r equaled 0.97% (SD = 2.03). Most of the variability of the q_c values comes from one set (#3, Date 13), where one quarter of the fish were caught. We tested the two q measures obtained for this set (24.2, 6.85) as outliers in their respective series (Dagnélie 1975, p. 34). With this procedure, the value to be tested was initially removed from the data, and a new mean and standard deviation were calculated (q_c' = 1.20, SD = 1.63). A Student's t statistic was then calculated (15.3 and 4.4 respectively) and compared with the 5% critical value $t_{0.05}$ = 3.6. This allowed us to discard the data from set #3. After removal of the outlier set, the difference between the two estimations of q, tested using the Wilcoxon's signed rank test, was not significant at the 0.05 level. Thus, the 39 measures of q were pooled for the calculation of the mean (q = 0.93) and SD = 1.58. The efficiency was then calculated using Equation 1 to be 12% ($e = 0.93 \cdot 9.4/0.72$).

For *T. guineensis*, the two catchability estimation methods yielded the following results: using the method from captures (Table 6), the mean, noted q_c equaled 3.54 (SD = 1.70) and from recaptures (Table 7), the mean, noted q_r, equaled 1.39 (SD = 1.44).

We compared the two samples (Wilcoxon's rank test) and found a highly significant difference (P = 0.01). The q_r value was considered to be more reasonable and the reasons will be discussed later. The efficiency follows was then calculated to be 18% ($1.39 \cdot 9.4/0.72$).

Avoidance of the Purse Seine

The avoidance rate (u) was estimated using Equation (2), $e = u \cdot v \cdot w$ (pooled mean from Table 2), knowing e, w, and with v being equal to 1 in our experimental conditions. For *Chrysichthys* spp., e = 0.12 and w = 0.73, thus, $u = e/w$ = 0.16. Thus active avoidance rate appears to be the main factor in the efficiency. For *T. guineensis*, the q_r estimation from recaptures

TABLE 6.—Estimation of the catchability relative to the purse seine by the method "from captures" (c_i = purse seine captures; N_i = standing stock; q_i = catchability %; C = beach seine catches; W = beach seine retention rate).

Dates (Oct. 1984)		Set numbers 1	2	3	4	5	6	C,W
Chrysichthys spp.								
8	c_i	4	1	13	6	15		149
	N_i	310	306	305	292	286	271	0.55
	q_i	1.29	0.33	4.26	2.05	5.24		
9	c_i	0	10	0	0	0		1,031
	N_i	1,367	1,367	1,357	1,357	1,357	1,357	0.76
	q_i	0	0.73	0	0	0		
13	c_i	3	0	32	4	1		56
	N_i	135	132	132	100	96	95	0.59
	q_i	2.22	0	24.2	4.00	1.04		
16	c_i	0	2	1	2	5		202
	N_i	641	641	639	638	636	631	0.32
	q_i	0	0.31	0.16	0.31	0.79		
Tilapia guineensis								
8	c_i	16	17	9	26	28		165
	N_i	480	464	447	438	412	384	0.43
	q_i	3.33	3.66	2.01	5.94	6.80		
16	c_i	3	5	9	5	3		47
	N_i	193	190	185	176	171	168	0.28
	q_i	1.55	2.63	4.86	2.84	1.75		

TABLE 7.—Estimation of the catchability by the purse seine by the method "from recaptures" (m_i = marked fish; r_i = recaptured fish; q_i = catchability, as a percentage).

Dates (Oct. 1984)		Set numbers 1	2	3	4	5
Chrysichthys spp.						
8	r_i	0	0	0	0	1
	m_i	16	16	16	16	16
	q_i	0	0	0	0	6.25
9	r_i	0	0	0	0	0
	m_i	78	78	78	78	78
	q_i	0	0	0	0	0
13	r_i	0	0	10	3	0
	m_i	146	146	146	136	133
	q_i	0	0	6.85	2.21	0.00
16	r_i	0	0	1	1	2
	m_i	100	100	99	98	97
	q_i	0	0	1.01	1.02	2.06
Tilapia guineensis						
8	r_i	1	5	1	1	3
	m_i	133	112	107	106	105
	q_i	0.88	4.46	0.93	0.94	2.89
16	r_i	1	0	0	1	0
	m_i	53	52	52	52	51
	q_i	1.89	0	0	1.92	0

yielded $e_r = 0.18$ and $w = 0.54$ (Table 2), thus, $u_r = 0.33$. According to these results, the purse seine seems comparably efficient for both species (12% and 18%), but the avoidance and the escapement rates are very different.

Species and Size Selectivity

The total catches by the purse seine (25 sets) and by the beach seine (5 sets) are summed in Table 8, along with the ratio of these values. Important difference appear between the ratios for the 16 species listed. They range between 0.003 and 0.17; this will be termed "species selectivity".

The same ratio was also computed by size group for seven species and analyzed using a Kruskall-Wallis one-way analysis of variance (Table 9). A large size effect, termed here "size selectivity", appears for *T. guineensis* and is likely for *Gerres nigri*, but is not significant for the other species.

TABLE 8.—Total catches in number by purse seine (PS) and beach seine (BS) during the whole experiment. The mean ratio of catches per set by both gears is calculated with the coefficient of variation (C.V.) expressed as a percentage.

Species	PS	BS	Ratio	C.V.
Gerres nigri	167	8,591	0.0039	130
Pomadasys jubelini	6	143	0.0084	101
Tylochromis jentinki	22	366	0.0120	32
Chrysichthys auratus	139	2,232	0.0125	127
Chrysichthys maurus	26	384	0.0135	120
Chrysichthys nigrodigitatus	9	96	0.0187	127
Caranx hippos	2	17	0.0235	132
Elops lacerta	135	1,049	0.0257	39
Arius latiscutatus	6	32	0.0375	173
Ethmalosa fimbriata	1,958	8,816	0.0444	37
Trachinotus teraia	11	44	0.0500	148
Sarotherodon melanotheron	27	81	0.0667	156
Callinectes amnicola	96	137	0.1401	261
Citharichthys stampflii	61	75	0.1627	145
Tilapia guineensis	362	437	0.1657	18
Penaeus notialis	1,234	32	7.7125	92
Total	2,973	22,963	0.0259	

DISCUSSION

The validity of the different results depends to a large extent on the robustness to departures from the underlying assumptions: no marking and holding stress, no mortalities, and no enclosure effect (e.g., accessible stock may differ from the standing stock if fish are crowded along the enclosure).

Escapement

For the *Chrysichthys* spp., the estimates of the retention rates are consistent with estimates of catchability and seem valid. On the other hand, for *T. guineensis*, the retention rates lead to unexpected results on three occasions ($W_1 > W_2$, Table 4). Marked-1 fishes escaped less than

TABLE 9.—Comparison of the catches per set by both gears, by size group, using a one-way analysis of variance by ranks (Kruskall-Wallis test). Critical value of $\chi^2_{0.95}$ is 7.81.

Species		Size group 1	2	3	4	χ^2_{obs}
Tilapia guineensis	R	1.127	0.804	0.556	0.154	12.78
	C.V.	35	23	48	32	
Gerres nigri	R	0.012	0.023	0.036	0.102	6.15
	C.V.	105	130	99	54	
Elops lacerta	R	0.144	0.092	0.113	0.244	0.09
	C.V.	18	181	87	32	
Ethmalosa fimbriata	R	0.202	0.454	0.376	1.091	2.38
	C.V.	58	1,289	166	201	
Chrysichthys auratus	R	0.065	0.065	0.030	0.077	3.44
	C.V.	130	164	181	235	
Chrysichthys maurus	R	0.162	0.040	0.029	0	5.82
	C.V.	175	294	84		
Chrysichthys nigrodigitatus	R	0.087	0	0.187	0.080	2.30
	C.V.	57		140	163	

marked-2 ones, even though they spent more time inside the beach seine and thus had more opportunities to escape. To explain this result, consider how the two sets of marked fish might have differed: 1) by sampled sizes, 2) by the type of mark, and 3) by the duration of the holding period. Sampling of sizes does not need to be examined because there was no significant correlation between the size and the retention rate. The type of mark itself did not seem likely to influence the fish behavior. However, the duration of the holding period was much longer for marked-1 fish, increasing the opportunities to escape and thus to overestimate W_1. For *T. guineensis*, the two q estimations (Tables 6, 7) differed to a large degree. This was probably due to the stress on marked-1 fish, leading to an overestimation of W_1, and thus to an overestimation of the catchability (q_c) calculated by the capture method. The W value that would produce a catchability estimate of $q_r = 1.39\%$ has been calculated iteratively and equals 14%. This retention rate is very low but is consistent with the known behavior of this cichlid species, which escapes from beach seines by slipping under the lead line and by jumping over the net (to recover the jumping fish, local fishermen often place small canoes equipped with net curtains along the seine).

In any case, a retention rate estimated with a marking procedure is greater or equal to the actual efficiency and can be used as an upper estimate of the efficiency. For example, efficiency of the purse seine for the crab *C. amnicola* is smaller than the observed 10% retention rate (Table 3).

The comparison of the retention rates for both seines indicates that the purse seine is more efficient in limiting escapement than the beach seine. This can be explained to some extent by the difference in the duration of the sets (22 minutes versus 6 hours). The rigging of the gears may also have an influence; the purse seine lead-line hugs the bottom, owing to the drag and weight of the rings, more efficiently than the beach seine; noise and vibrations in the ropes also generally keep the fish away from the net (Hemmings 1967). Therefore, pursing is more efficient than the manual closing of the beach seine. The better efficiency of the purse seine should, however, not be generalized because the efficiency of a particular gear may be influenced by subtle differences of rigging (MacMullen 1981). We did observe during another experiment[3] some important differences in the efficiencies of two apparently similar purse seines, probably resulting from a slight difference in lead-line weights.

Species and Size Selectivity

Other robust results came from a comparison of the catch rates of the two gears in terms of species relative abundance (species selectivity) and size distribution (size selectivity).

Species selectivity is due to differences between the efficiencies, which depend upon complex interactions between the gears and the behavior of the species. In this experiment, an additional "enclosure effect" can happen if all fish are not equally available. For instance, by crowding along the net, the fish become inaccessible to the purse seine (p_A, the overall accessibility is then less than 1).

The ratio of catch rates by the two gears, calculated in Table 8, can be compared to the theoretical value that would be obtained if both gears were equally efficient, and if the avoidance rate for beach seine was negligible. This can be assumed as a first approximation since the net is very large (1,100 m) and fairly silent (no engine was used in the boat).

From the formulas given above (see methods: estimation from captures):

$$c_i = \frac{q \cdot C}{W} \cdot \frac{1}{(1-q)^{6-i}} \qquad \text{and} \quad r = \frac{q}{W} \cdot \alpha,$$

$$\text{with } \alpha = \frac{1}{(1-q)} + \frac{1}{(1-q)^2} + \ldots + \frac{1}{(1+q)^5}$$

since $q = p_a \cdot e$, then $r = p_a \cdot (e/W) \cdot \alpha$.

The parameter r appears to be roughly proportional to e/W, α being a correction factor accounting for the successive catches in the enclosure. The parameter α, depending on the value of e, which varies between 0 and 1, is in the interval (1–1.276). If the efficiencies of the two gears are equal ($e = E$ or $e = W$, since U is assumed to be equal to 1), r is in the interval $[p_a - 1.276 \cdot p_a]$, that is [0.076–0.097]). In Table 8, r is smaller than 0.076 for most fish species, indicating lower efficiency of the purse seine. On the contrary,

[3]Cantrelle, I., E. Charles-Dominique, Y. N. N'Goran, and J. Quensière. 1983. Etude expérimentale de la sélectivité de deux sennes tournantes et coulissantes (maillage 25 mm et maillage mixte 14–25 mm) en lagune Aby (Côte d'Ivoire). Unpubl. rep., 36 p. Cent. Rech. Océanogr, Abidjan.

the purse seine is more efficient for the burrowing species (*Callinectes* spp., *Citharichthys stampflii*, *Penaeus notialis*) and for *T. guineensis*.

Size selectivity appears for two species (*T. guineensis* and *G. nigri*) when the ratio of catches is calculated by size group (Table 9). As it has been shown above for the marked species, the size composition of fishes in the enclosure during the experiment does not differ from that of the final catches of the beach seine. Two factors remain explaining this size selectivity: 1) a size selective accessibility within the enclosure and 2) a size selective catchability by the purse seine. The first factor is impossible to assess. The second one may happen with active gear, like the seines. Larger individuals may be better able to avoid capture because of their higher maximum swimming speed (Bainbridge 1958; Blaxter 1967). This type of size selectivity has been shown in sampling plankton larvae with an experimental active gear (Murphy and Clutter 1972), and may here explain the decrease in the ratio of the catch rates with size in *T. guineensis*.

In *G. nigri*, the selectivity is reversed, small sizes being underrepresented in the purse seine catches. This point seems difficult to interpret, and probably complex mechanisms are involved: enclosure effect (size-dependent accessibility) and size dependent catchability owing to complex behavior. Some descriptions of complex behavior of fish during a fishing operation are given in the literature. For trawlers and Danish seines, the flight is triggered by a stimulus, mainly visual, from the moving gear at a certain distance (MacMullen 1981). Different species react differently; some demersal species jump perpendicularly, while others jump in random directions (Hemmings 1967). Anchovies surrounded by a purse seine tend to move into deeper waters (Inoue and Ayodhyoa 1967).

Efficiency

For the results of the efficiency measurement to be valid, all of the assumptions must be met. Consequently, efficiency estimates may not be completely reliable.

Efficiency of the purse seine for fishes larger than L_{100} is very low according to our results (*Chrysichthys* spp., 12% and *T. guineensis*, 18%). Actually, purse seining is an efficient technique when based on spotting and surrounding pelagic fish schools. However, it probably becomes very inefficient for "blind" fishing of demersal species, as was done in this experiment and as is often practiced in Ivory Coast lagoon fisheries. The main cause of this inefficiency is most likely the avoidance during the surrounding phase of the operation.

The efficiency of a large, nonmotorized beach seine, reaching the ground in shallow waters, depends mostly on a low escapement rate after closing the net. Estimation of the escapement rate by mark-recapture can thus provide a simple and reliable upper estimate of efficiency. However, it is important to stress that a general application of such values to the entire fishery is not possible unless the variability of gears and fishing grounds is considered.

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Otoconia From Four New Zealand Chimaeriformes

K. P. Mulligan, R. W. Gauldie, and R. Thomson

ABSTRACT: A scanning electron microscopy and x-ray diffraction investigation of chimaeriform otoliths shows densely packed and strongly bound aggregations of otoconia in the form of aragonitic spherulites. Characteristic sizes, shapes, and surface features are described for each of the four species investigated. Otoconial diameters differ among species, but the chimaeras are nonetheless a uniform group in terms of otoconia type and otolith shape.

Members of the Class Chondrichthyes (elasmobranchs and Chimaeriformes) are known to have otoliths composed of otoconia bound in a protein matrix (Stewart 1903; Iseltöger 1941; Carlström 1963; Barber and Emerson 1980). The use of the term otolith in reference to chondrichthyan fish requires some clarification. There are difficulties in establishing chemical or crystalline homologies between aggregated otoconia and otoliths proper as they occur in teleosts. However, they are similar in being semirigid or rigid structures supported on a hair cell pad and involved in sound transduction in both elasmobranchs and teleosts (Popper and Fay 1977; Fay 1983). When homologies are established, a general term for a crystalline, calcium carbonate structure associated with sound transduction may appear, but until then we will persist in using the term otolith in a more general sense than its derivation implies.

Studies on the otolith of the chimaera *Callorhynchus milii* (Callorhynchidae), which is found in inshore waters of New Zealand, showed that it was composed of fused spherulitic otoconia (Gauldie et al. 1987). Spherulite otoconia were one of three differing forms of otoconia, which were found in the Australian lungfish *Neoceratodus forsteri* (Gauldie et al. 1986a), and were similar to the type of free otoconia found in conjunction with the otoliths of some teleosts (Dale 1976; Gauldie et al. 1986b) and described in some shark species (Carlström 1963).

Spherulitic otoconia fused into otoliths have also been described in humans, occurring in association with hereditary deafness (Johnsson et al. 1981). Humans normally have only calcitic otoconia similar to those occurring in the lungfish, but apparently there are still human genes that will code for the spherulitic otoconia. It is tempting to see the widespread distribution of spherulitic otoconia as an indication that they are the most primitive kind of crystalline calcium carbonate secreted by the vertebrate ear. There are strong similarities between the shapes and anatomical arrangement of the otoliths in the chimaera *C. millii* and the lungfish *N. forsteri*, as well as in some of their constituent otoconia. These observations support the suggestion (Patterson 1965; Romer 1968) that the modern chimaeras might be descended from ptyctodont placoderms. Thus, apart from the issue of chimaera affinities within the elasmobranchs (Zangerl 1973), the spherulitic otoconia of the chimaeras may hold some clues to the fundamental mechanism of otolith deposition.

Several species of deep-water chimaeras occur in New Zealand's waters. Otolith form and structure from the two families Rhinochimaeridae (*Harriotta raleighana* and *Rhinochimaera* sp.) and Chimaeridae (*Hydrolagus novaezelandiae* and *Chimaera* sp.) are investigated in this paper.

MATERIALS AND METHODS

Three specimens of each species—*H. raleighana*, *Rhinochimaera* sp., *H. novaezelandiae*, and *Chimaera* sp.—were caught in a deep-water trawl survey of the Chatham Rise area, December 1985. Heads were placed in a 10% neutral buffered formalin solution for 24 hours and transferred to 70% isopropanol until dissection. The preservative solutions remained alkaline during storage time, but after more

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lengthy periods (more than 6 months), 70% isopropanol became weakly acidic with a pH of 6.5–6.7. All otic complexes were removed from heads within three weeks of initial fixation. Samples were then photographed with a Wild M400[1] photomicroscope before their otoliths were removed in preparation for scanning electron microscopy (SEM). Selected whole and fractured portions were then dehydrated in an ethanol series, mounted on stubs with a metallic cement, and sputter-coated with gold under five atmospheres of pressure before being viewed on a Philips 505 SEM.

Analyses of samples by x-ray diffraction were carried out on a Philips PW1279/PW1710 x-ray diffractometer. Operating conditions for the diffractometer were the following: 45 kV for the Cu tube; 40 mA for the automatic divergence slit; 0.1 mm for the receiving slit; 1° for the scatter slit; and a Ni filter. Goniometer speed was set at 3°2θ/min, and chart speed was set at 10 min/°2θ from 5 to 55°2θ. The error of estimated proportion of calcium carbonate morph (calcite, aragonite, and vaterite) was ±5%. Otoconial diameters were directly measured from SEM photographs.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

RESULTS

The general shape and organization of the four chimaeriform otic complexes (including semicircular canals and otoliths) resembled the shape and organization of *C. milii* (Gauldie et al. 1987). Two otoliths occurred within a single sac, oriented at more or less right angles to each other, and presumably corresponded with the sagitta and astericus of teleosts. All of the otoliths described in this study were the sagittae.

The otoliths of the Chimaeriformes were solid masses of aggregated otoconia (Fig. 1A, B, C). Otoliths of *H. novaezelandiae* had densely packed central areas with looser aggregations of otoconia on the exterior surface (Fig. 1B). The matrix was less apparent in *H. raleighana*, and the otolith was characterized by many small otoconia (Fig. 1C), giving a loose granular appearance, while *Rhinochimaera* sp. otoliths (Fig. 2A) had closely packed arrays of otoconia. *Chimaera* sp. otoliths (Fig. 2B) were solidly packed with less cohesive matrix material visible.

FIGURE 1A.—*Rhinochimaera* sp. otolith. Bar = 1 mm.

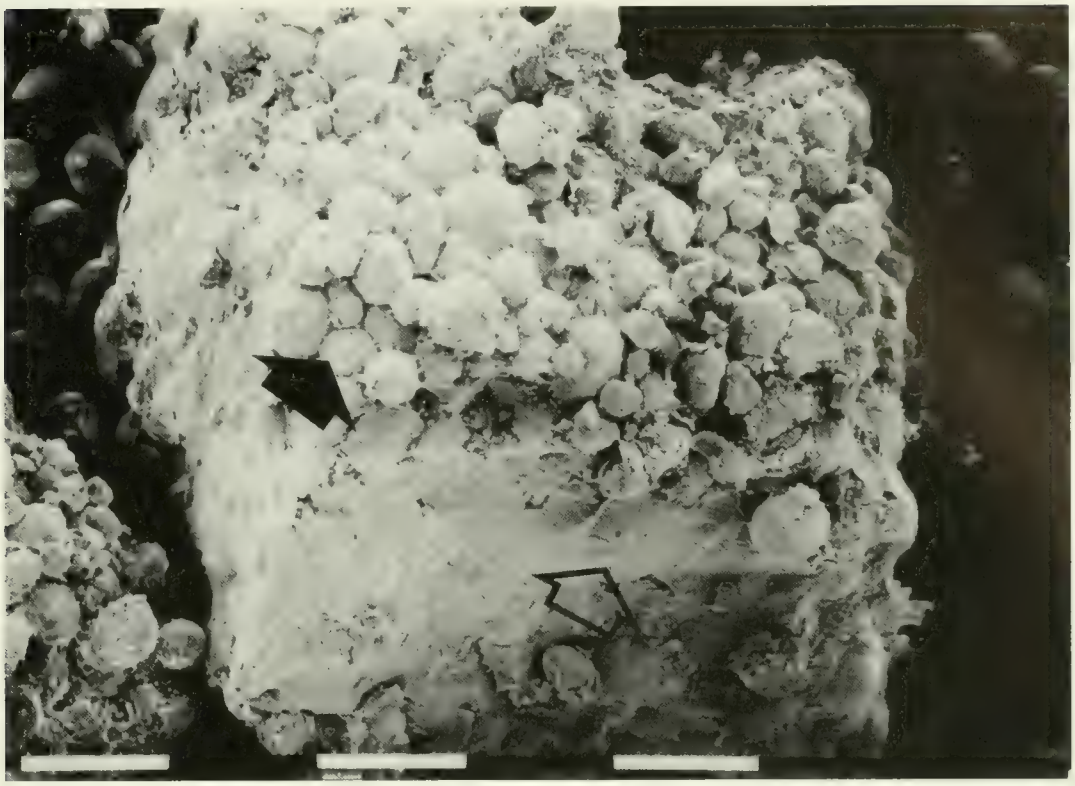

FIGURE 1B.—Broken portion of central mass of *Hydrolagus* otolith. Closed arrow indicates pockmarked features on the surface of the otoconium. The internal morphology of otolith consists of otoconia fused together (open arrow). Bar = 0.1 mm.

FIGURE 1C.—Mass of otoconia from *Harriotta*. Bar = 1 mm.

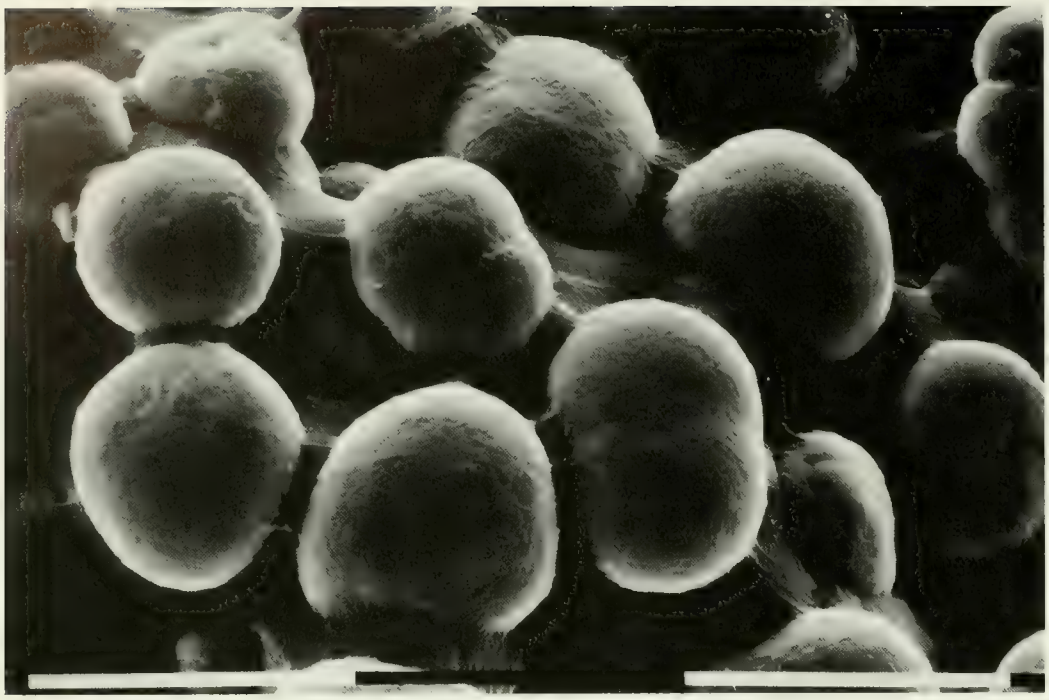

FIGURE 2A.—*Rhinochimaera* sp. otolith showing the encapsulation of otoconia by the matrix. Bar = 0.1 mm..

FIGURE 2B.—Otoconia of *Chimaera* sp. have little encapsulating matrix. Bar = 0.1 mm.

A dense aggregation of otoconia occurred within the otoliths of *Rhinochimaera* sp., each otoconia having a distinctive pockmarked surface topography (Fig. 3A). Surface otoconia (see Figure 2A) lacked these pockmarked features. At high magnifications, the pockmarked surface could be seen more clearly (Fig. 3B). In some cases the pockmarks resulted in enough material being removed from the surface to show that otoconia were deposited as layers (Fig. 3C). A few otoconia showed small ($\simeq$ 1 μm) spherules on their surface and some indications of fusion of the spherules into a distinct layer (Fig. 3B, D). Broken otoconia showed the expected epitaxial growth of crystals from a central point. The growth of individual otoconia appeared to be parallel to that of the otolith: small spherules ($\approx$ 1 μm) continued to grow (1 μm) and progressively fuse into larger otoconia, which in turn fused to the form of the otolith itself (Fig. 3E).

The otoconia from *H. novaezelandiae* had a greater size range than those of *Rhinochimaera* sp. and *H. raleighana* and were more oval in shape. Although small ($\simeq$ 1 μm) spherules occurred on the surface of otoconia, they did not assume the more coordinated, layered appearance seen on the otoconia from *Rhinochimaera* sp. and may have represented recrystallization.

At similar magnifications to *Rhinochimaera* sp. and *H. novaezelandiae*, individual otoconia of *H. raleighana* showed a smooth and uniform surface. However, numbers of small crystals with variable shapes were commonly found in the otoconial mass of *H. raleighana*. Among these crystals were many rod-shaped and twinned rod-shaped crystals, some of which had small, surface recrystallizations on them (Fig. 4A). Crystalline aggregations occurred amongst the *H. raleighana* otoconia, which had the appearance of being part spindle-shaped aragonite crystal, part aragonite spherule, and part fused rod-shaped crystal (Fig. 4B).

The majority of otoconia observed from *Chimaera* sp. were regular spheres. On closer examination, the surfaces of *Chimaera* sp. otoconia varied from smooth to crystalline, and some otoconia surfaces exhibited a highly textured, irregularly crenellated surface (Fig. 5A). Deposits of irregularly formed otoconia occurred in *Chimaera* sp.; they were marked by the absence of any readily observable matrix binding and by the appearance of partially eroded

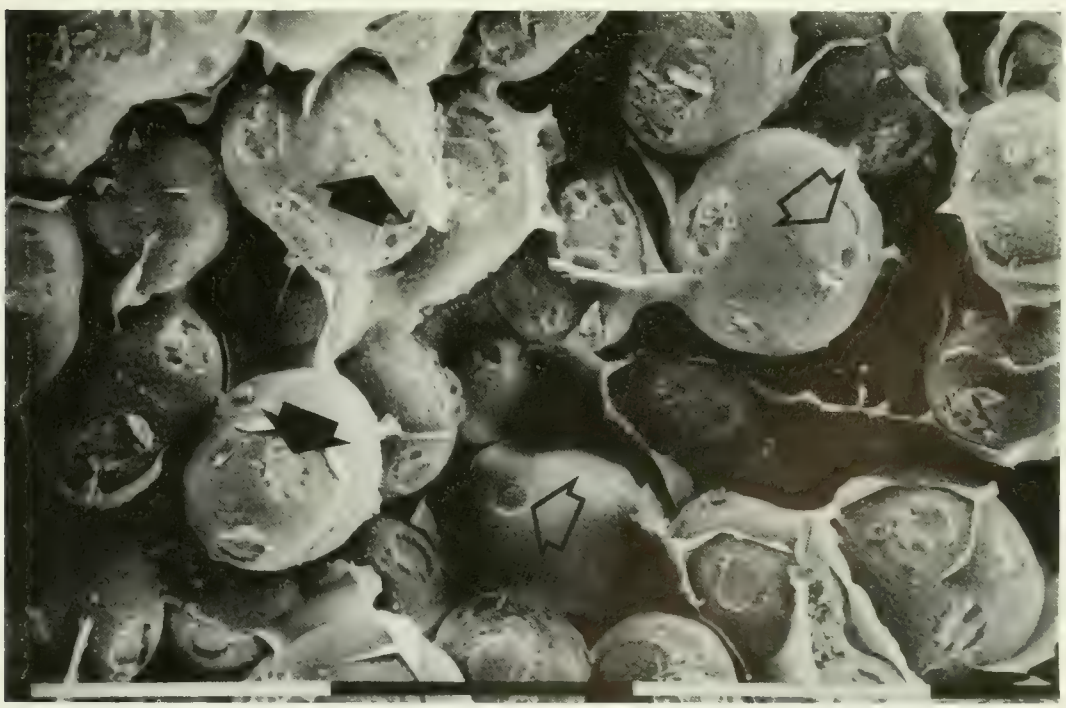

FIGURE 3A.—Otoconia from *Rhinochimaera* sp. have a distinctive pockmarked appearance, that shows possible points of adhesion (closed arrows) and other occurrences on the surface of the otoconia (open arrows) Bar = 0.1 mm.

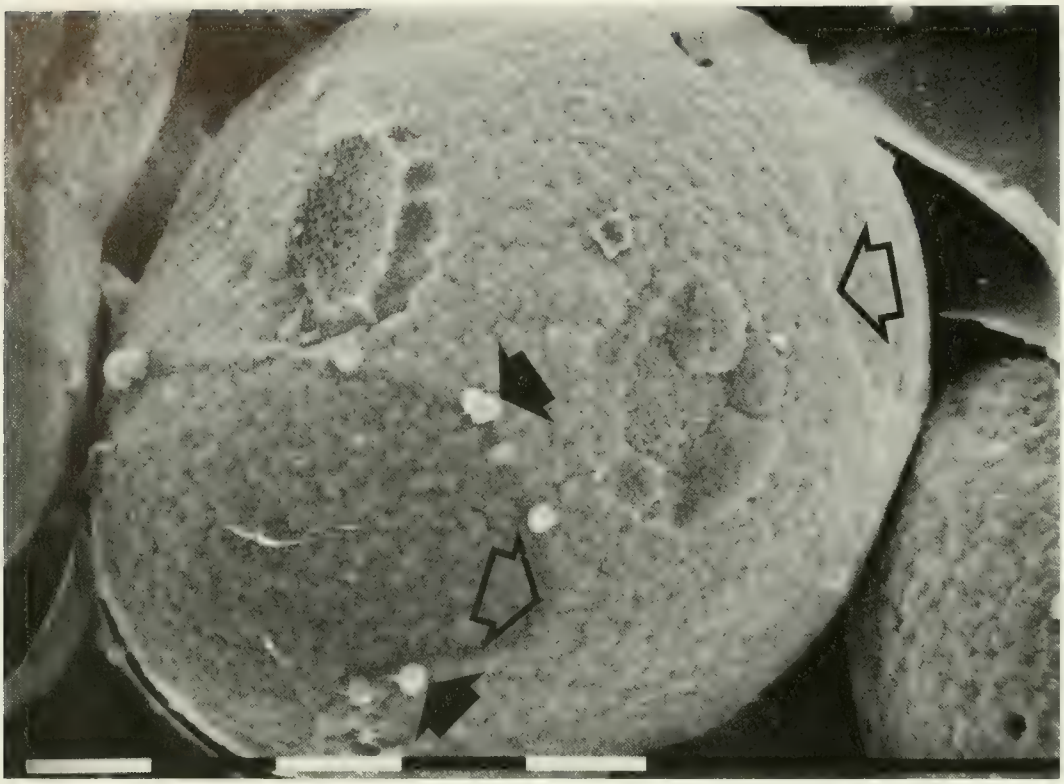

FIGURE 3B.—Small spherules (arrows) appear on the surface of the otoconia from *Rhinochimaera* sp. The body of the otoconia itself appears to be formed by the fusion of such small spherules, which may account for the smoothly bounded depressions (open arrows) on the surface as well as for the more obvious pockmarks. Bar = 10 μm.

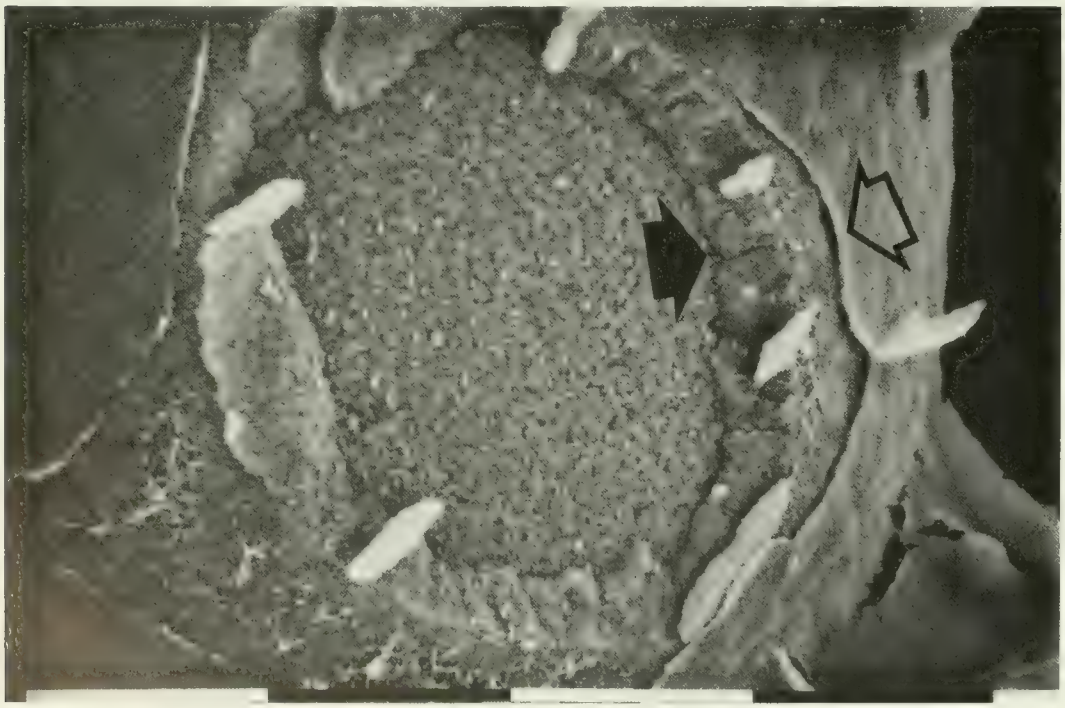

FIGURE 3C.—Small *Rhinochimaera* sp. otoconia show an apparently layered surface (closed arrow) and an enveloping matrix (open arrow). Bar = 10 μm.

FIGURE 3D.—Some otoconia from *Rhinochimaera* sp. have surfaces formed of many small (≃ 1 μm) spherules which have yet to fuse to form the next smooth layer of surface. Bar = 10 μm.

FIGURE 3E.—Broken otoconia from *Rhinochimaera* sp. show a radiating crystal structure with faint traces of small spherules (arrows). Bar = 0.1 mm.

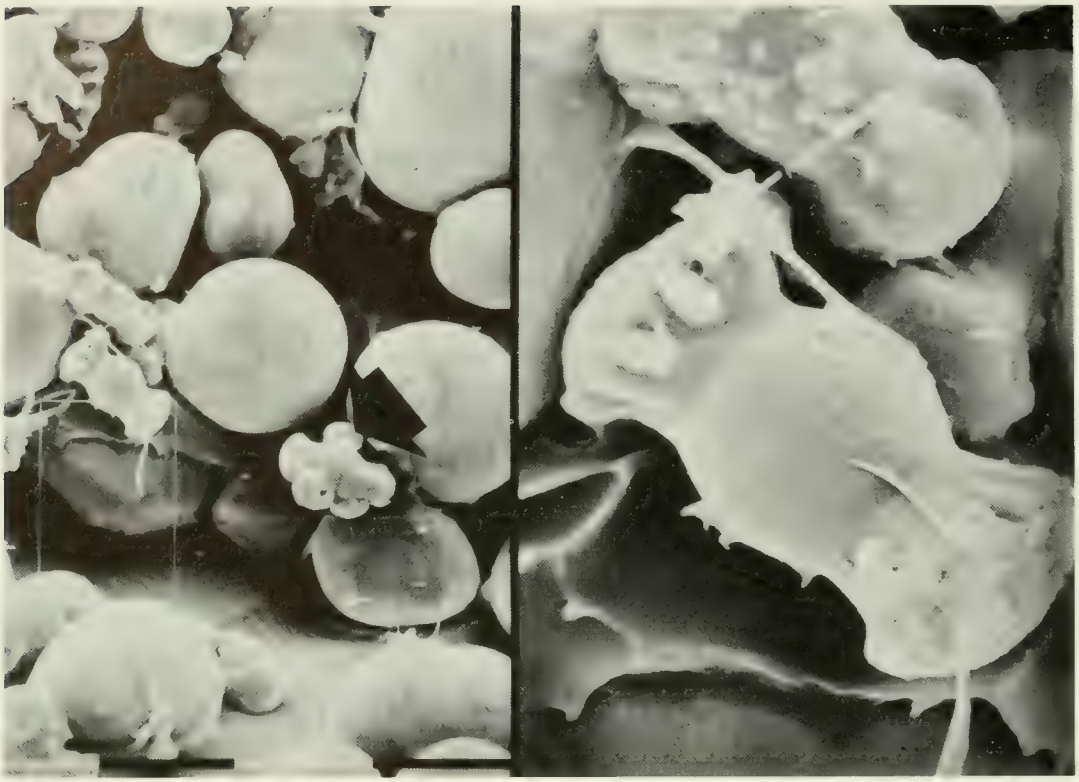

FIGURE 4A.—The round otoconia of *Harriotta raleighana* are very smooth compared with the otoconia of other chimaeras. An unusual rod-shaped crystal occurs in association with the otoconia which has a single (small closed arrow) and twinned (large closed arrow) form. In the higher magnification section the rod shaped crystals show further recrystallization on their surfaces. Bar = 10 μm.

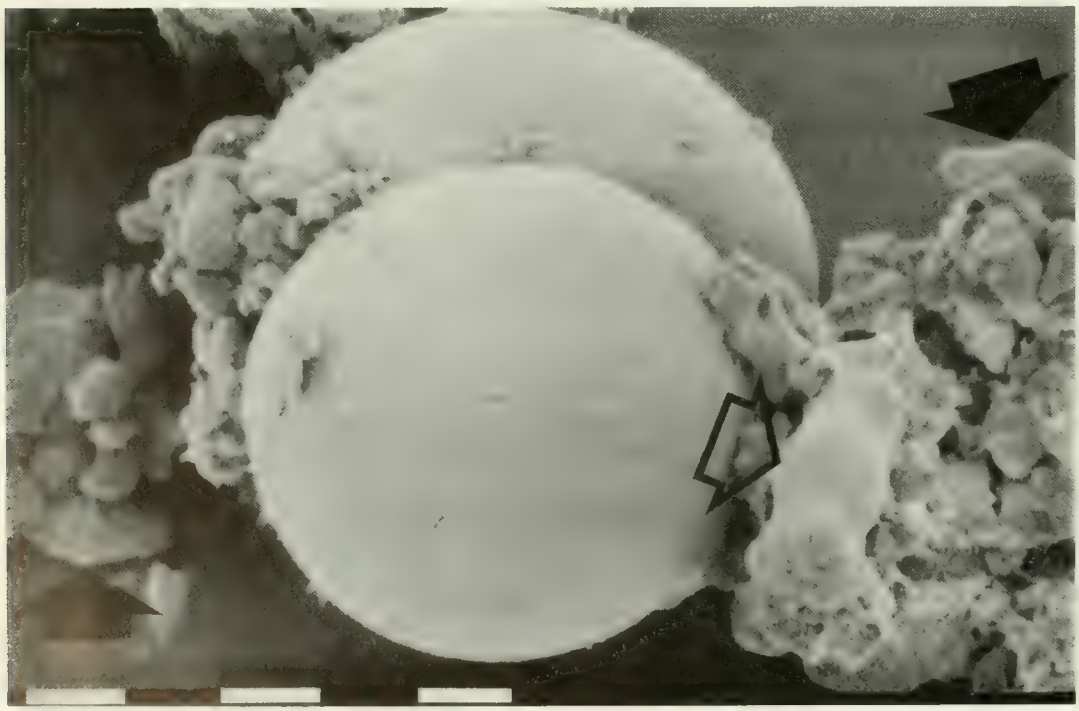

FIGURE 4B.—Crystalline aggregates of the rod-shaped crystal (open arrow) and apparent aragonite spindles (closed arrows) are found in association with the typical aragonite spherule type crystals. Bar = 50 μm.

spindle-shaped aragonite crystals (Fig. 5B). X-ray diffraction studies of the chimaeriform otoconia examined, including *Chimaera* sp., indicated that all of the calcium carbonate present was in the aragonite form.

Mean otoconial diameters of all four species of

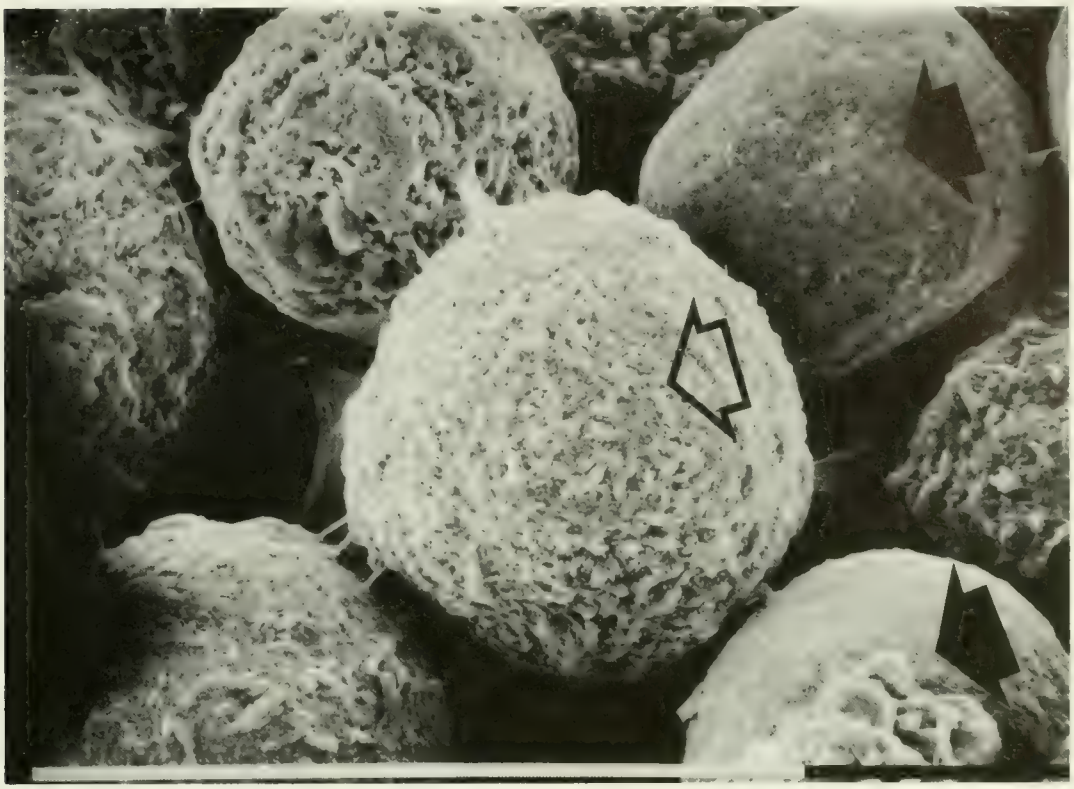

FIGURE 5A.—Otoconia from *Chimaera* sp. include both smooth (closed arrows) and highly textured (open arrow) otoconia. Bar = 0.1 mm.

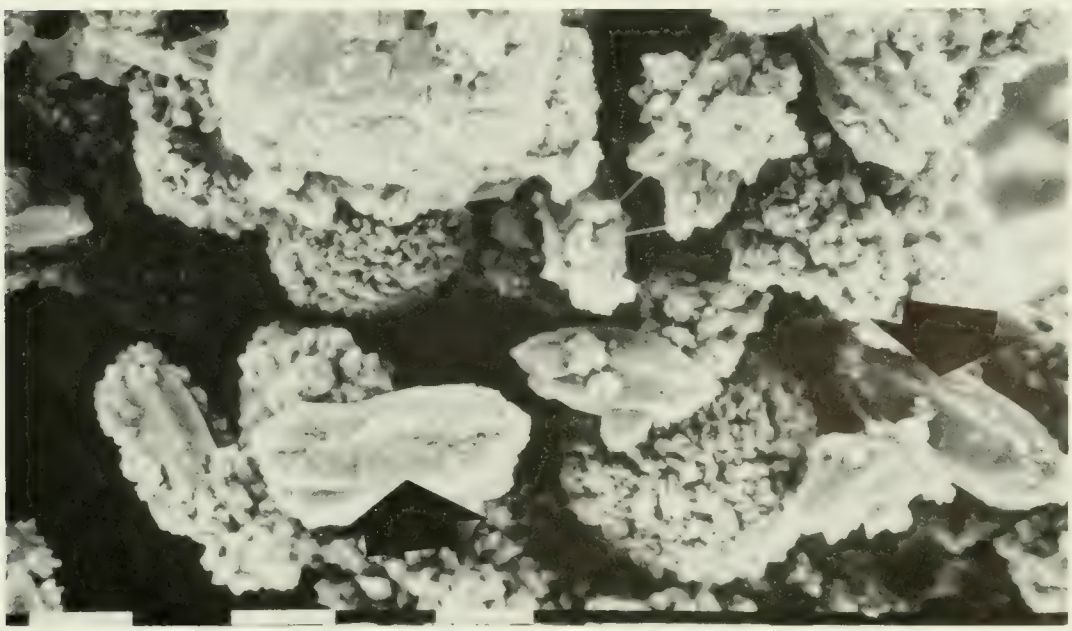

FIGURE 5B.—Parts of the otolith of *Chimaera* sp. are composed of small otoconia of the highly textured type as well as what appear to be partially eroded free aragonite crystals (arrows). Bar = 10 μm.

Chimaeriformes are listed in Table 1. A *t*-test weighted for unequal variances (Sokal and Rohlf 1969) shows statistically significant differences in the diameters of otoconia from different species ($P \leq 0.05$).

TABLE 1.—Mean otoconial diameters (μm) of all four species of Chimaeriform fish. n = sample size, $\bar{x}$ = mean otoconial diameter, SD = standard deviation.

Species	n	$\bar{x}$	SD	t	$t(.05,49)$
Rhinochimaera sp.	50	66.72	4.91		
				→3.6756	
Harriotta raleighana	50	62.19	7.20		2.0094
				→9.1056	
Chimaera sp.	50	50.26	5.83		
				→1.4738	
Hydrolagus novaezelandiae	50	48.19	8.04		

DISCUSSION

Carlström (1963) described the otoconia of *Chimaera monstrosa* as "almost perfect aragonite spheres". This study at the SEM level confirmed the generally spherical nature of chimaeriform otoconia that was observed at the light microscope level, and revealed considerable detail in variation in size, shape, and crystallinity of otoconia from four species of chimaeriforms.

There was a statistically significant variation in the diameters of otoconia amongst the species examined. In part, this variation reflected the relative amounts of small and large otoconia in the different species, as well as the maximum size of otoconia. Size variation in otoconia may represent physiological differences between individuals of the same species, interspecific differences, and perhaps age differences. Testing these alternatives was not possible with the samples at our disposal.

The predominant type of otoconia among the samples examined was more or less spherical, 40–70 μm in diameter. It was similar in size and in shape to otoconia described in the lungfish (Gauldie et al. 1986a), in the chimaera *C. milii* (Gauldie et al. 1987), and in a number of teleost species (Dale 1976; Gauldie et al. 1986b). X-ray diffraction studies showed that the spherule otoconia were formed from aragonite. Aragonitic spherule otoconia occurred in the chimaera *C. milii* (Gauldie et al. 1987) and in the lungfish *N. forsteri* (Gauldie et al. 1986a). However, spherule shaped otoconia composed of vaterite have been described in the shark *Somniosus pacificus* (Lowenstam 1980), albeit with a distinctive polycrystalline appearance at the SEM level that is distinctively different from the aragonite spherule otoconia of chimaeras.

The rod-shaped crystals found in the otoconial mass of *H. raleighana* have not been described in the literature. It is possible that they were bacteria or some other organism. However, their crystalline appearance, which included twinning and surface recrystallization (Fig. 4B), as well as their apparent fusion with the spindle and spherule forms of aragonite, strongly suggest that they are some form of crystal.

There was considerable variation in the surface texture of the otoconia amongst the species described here and those described elsewhere. The otoconia of *H. raleighana* had the smoothest surface texture, but were among the larger otoconia. Therefore, one could reasonably conclude that variation in surface texture may not be due to the rate of crystal growth. In addition, otoliths of *Chimaera* sp. consisted of otoconia of about the same size, but with greatly differing surface texture. We have assumed that during storage the fluids of the endolymphatic sac were alkaline, but it is possible that in the stress of trawling the endolymph may have become acidic. Thus, variation in surface texture may be a preservation artifact. However, the similarity of the appearance of the surface texture of otoconia to those described from other studies, using different preservation techniques, suggests that erosion and recrystallization had not occurred. We conclude that the texture of the otoconia surface does not reveal any useful information about the growth rate of otoconia, but that it may provide clues to probable growth mechanisms.

For example, the layered appearance of some

otoconia may have been due to incremental growth. It was similar to the layered appearance of the lungfish otoconia (Gauldie et al. 1987) and to the layered appearance of statoconia in some mollusc species (Geuze 1968). If there was incremental growth of the otoconia, it indicates that, even at the most primitive level, the calcium metabolism of the inner ear has a definite periodicity. However, there is a major difference between the growth process of otoconia in the chimaera and that of statoconia in the mollusc (Kuzirian et al. 1981): the aragonitic otoconia of the chimaera obviously grows (and fuses into an otolith) in situ. The otoconia of the chimaera otolith often showed small surface crystals that apparently fuse together, implying continuous growth in situ, which is characteristic of teleost otoliths.

It can be assumed that a rigid otolith is required if the otolith functions as a sound transducer (Fay 1983) and that, in contrast, a loose aggregation of otoconia serves as a tilt, or angular momentum detection mechanism (Marmo 1983). The otoliths of the four species described here are rigid in comparison to those of *C. milii* (Gauldie et al. 1987), less rigid than the lungfish otoliths (Gauldie et al. 1986), and much more rigid than the loose and friable aggregations of otoconia that occur in most sharks and rays (Mulligan and Gauldie 1989). One might therefore conclude from our observations that the otoliths of chimaerids were functionally at a stage between a rigid sound transducer of the teleost type (which is found also in the lungfish) and an angular momentum detection mechanism.

The presence of spindle-shaped aragonite crystals in the otolith of *Chimaera* sp. is a particularly interesting observation because both spindle-shaped and spherule-shaped aragonite otoconia occur together with calcite crystals in the lungfish otolith. "Aragonite spherule" otoconia have also been described for the primitive shark *Heptanchus cinereus* (Nishio 1926) and have been observed (Mulligan and Gauldie 1989) in the related *Heptranchias perlo* of New Zealand waters. Furthermore, aggregated spherulitic otoconia have been observed in humans with congenital hearing disorders (Johnsson et al. 1981) and are difficult to distinguish visually from otoconial aggregations in chimaeras and some teleosts (Gauldie et al. 1986b).

It is tempting to see parallels between the otoconia of chimaeras, lungfish, and primitive sharks. However, the nature of evolutionary processes (particularly convergence processes) does not allow simple extrapolation of "primitive" features, and hence phylogenetic reconstruction, from modern species (Cain 1983). This is particularly true when the physiological effects of otoconia types on inner ear function are completely unknown. However, it is clear that the spherulitic otoconia and otic organization of chimaeriform fish have chemical and anatomical parallels with the inner ear of teleost fish in the orders Cheilodactylidae, Moridae, Gadidae, Balistidae, and Gempylidae; with some sharks; and, rarely, with humans. The occurrence of spindle shaped aragonite otoconia in conjunction with spherule otoconia has a parallel in the otoconia of the lungfish. Such similarities makes it very difficult to assign any taxonomic value to otoconia types. Perhaps spherulitic otoconia represent one of very few successful calcium carbonate matrix/mineralization systems which converge in so many vertebrates simply because there are so few alternatives.

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Feeding Habits of Whitebone Porgy, *Calamus leucosteus* (Teleostei: Sparidae), Associated with Hard Bottom Reefs off the Southeastern United States[1]

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ABSTRACT: The feeding habits of whitebone porgy, *Calamus leucosteus*, were investigated by examining stomachs of specimens collected from hard bottom reef habitat on the southeastern continental shelf and by comparing stomach samples with benthic samples and with stomach samples from four other sparids collected from the same habitat. Whitebone porgy were found to feed mainly on small hard-shelled species of gastropods, pagurid decapods, and sipunculids. Polychaetes, pelecypods, barnacles, and fishes were also eaten. Fishes and echinoderms were consumed by larger individuals. Whitebone porgy selected invertebrate species that were not abundant in benthic samples from the reef, suggesting that these fish forage on sand bottom fauna. Patterns of diet overlap with other reef-associated sparids appeared to be related to feeding morphology and feeding habitat. Overlap in diet between whitebone porgy and southern porgy, *Stenotomus aculeatus*, was low, although both species forage on sand bottom organisms. Pinfish, *Lagodon rhomboides*, fed mainly on a sessile reef amphipod that was rarely consumed by whitebone porgy. Whitebone porgy had a higher diet overlap with sheepshead, *Archosargus probatocephalus*, and with red porgy, *Pagrus pagrus*, because all three species fed on barnacles not consumed by other sparids examined.

The whitebone porgy, *Calamus leucosteus*, distributed from the Carolinas through the Gulf of Mexico (Randall 1978), is an abundant sparid fish on the continental shelf of the South Atlantic Bight, where it is an important component of trawl and hook-and-line fisheries (Huntsman 1976; Waltz et al. 1982). Whitebone porgy are found in depths of 11–88 m on the continental shelf of the southeastern coast of the United States, but they are most abundant in depths < 30 m (Waltz et al. 1982). The continental shelf at these depths consists primarily of sandy bottom, with occasional scattered outcrops of sedimentary rock (Struhsaker 1969), and, although whitebone porgy frequently occur on sand bottom, they are much more abundant in rocky reef habitats (Wenner et al. 1980; Waltz et al. 1982). These hard bottom habitats support a greater abundance and biomass of large sessile invertebrates (e.g., sponges, corals, tunicates) and associated motile organisms than do sand bottom areas of the shelf (Struhsaker 1969; Wenner 1983; Wenner et al. 1983; Sedberry and Van Dolah 1984; Wenner et al. 1984; Wendt et al. 1985). Many of these invertebrates serve as prey for fishes that are closely associated with the reef habitat (Manooch 1977; Sedberry 1987, 1988). Other species of fishes are less closely associated with hard bottom reefs, and, while living on or in proximity to these reefs, do much of their foraging in sand bottom habitats on the shelf (Sedberry 1985). Although whitebone porgy appear to be a reef-associated species, their dependence on reef habitat and the abundance of prey provided by these habitats are unknown. Although hard bottom reefs support a high biomass of potential prey for fishes, many species of predatory fish are concentrated in these habitats (Sedberry and Van Dolah 1984), and competition for prey may be intense, particularly among closely related species. Several other sparids are abundant in hard bottom reef communities and competition for food among these species could be as intense. Although the food habits of some of these more common sparids have been reported from offshore reef habitats (Manooch 1977; Sedberry 1987), overlap in diet among the species has not been investigated.

The purpose of this study is to describe the food habits of whitebone porgy, to determine the importance of hard bottom reef habitat as foraging grounds for this species, and to determine diet overlap between whitebone porgy and some

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other abundant sparid fishes from the same habitat.

METHODS

Stomachs of fish analyzed for food habits were collected during six trawl cruises on the continental shelf in 1980 and 1981. Stomachs of whitebone porgy were taken at 11 hard bottom stations distributed among 3 depth zones representing the inner shelf (16–22 m depth, three stations), middle shelf (23–37 m depth, four stations), and the outer shelf (46–69 m depth, four stations). Delineation of depth zones was based on distribution of fish and invertebrate species assemblages as noted in previous studies and on community analysis of trawl catches used in the present study (Struhsaker 1969; Miller and Richards 1980; Sedberry and Van Dolah 1984; Wenner et al. 1984). Fishes were collected primarily in trawl tows as described elsewhere (Sedberry and Van Dolah 1984; Wenner et al. 1984; Sedberry 1985). A few specimens were collected with trap or hook and line. Sampling for fishes was conducted on hard bottom habitat, which was mapped for each station using underwater television (Sedberry and Van Dolah 1984).

Whitebone porgy were measured (standard length, SL) at sea, and their stomachs were preserved in 10% seawater formalin. Contents of individual stomachs were then sorted in the laboratory by taxa, counted, and measured volumetrically. The relative contribution of food items to the diet was described by percent frequency occurrence (F), percent numerical abundance (N), and percent volume displacement (V). F, N, and V were calculated for prey species and for prey items grouped into higher taxonomic categories, for 50 mm intervals of SL.

In order to determine the selectivity or dependence of demersal fishes on hard bottom prey organisms, stomach samples were compared with benthic samples using Ivlev's index of electivity (Ivlev 1961). Electivity values range from -1 to $+1$. Negative values imply that the prey species is avoided by the predator or that it is unavailable to the predator. Positive values imply that the predator prefers the prey species or that it is feeding on prey species that occur in a different habitat than that sampled by the benthic sampler. A value near zero implies no selectivity by the predator; i.e., the fish is feeding on the prey in proportion to the prey's relative abundance in samples taken in the habitat.

The electivity index was calculated for species that were numerically dominant in benthic samples or in fish stomach samples which were pooled by depth zone (inner, middle, and outer shelves) for comparison. Benthic samples were obtained at the 11 hard bottom sites during 1980 and 1981 with a suction device (inner and middle shelves) or a grab (outer shelf). Divers obtained five replicate suction samples at each inner and middle shelf station by scraping the hard substrata enclosed by a 0.1 m^2 quadrat box, while simultaneously sucking with an airlift device similar to that described by Chess (1979). Suction samples were collected in 1.0 mm mesh bags. At the outer shelf stations where water depth precluded the use of the suction device operated by divers, quantitative samples (five copies) were collected with a 0.1 m^2 Smith-McIntyre grab. After retrieval, each sample was placed into a 1.0 mm sieve and washed to remove the finer sediment.

Sampling motile benthic invertebrates with the suction sampler proved to be a very simple, yet effective, technique. Samples were quantitative because suctioning effectively collected everything within the confines of the walled box placed on the substratum. The Smith-McIntyre grab, which was substituted for the suction sampler at deeper stations, was somewhat less quantitative because the sampler is not as effective on hard substrate, and the actual area sampled was unknown. In spite of these limitations, the grab sampler was the only feasible means of sampling the benthos at outer shelf stations and provided the only benthic collections with which to calculate electivity.

Similarity in diet between whitebone porgy and four other co-occurring and frequently collected sparids was also investigated. Stomach samples of these additional species were collected at the same time as the whitebone porgy stomachs and were analyzed in a similar manner (South Carolina Wildlife and Marine Resources Department 1984; Sedberry 1987). These other sparids were sheepshead, *Archosargus probatocephalus;* pinfish, *Lagodon rhomboides;* red porgy, *Pagrus pagrus*; and southern porgy, *Stenotomus aculeatus.*

Similarity in diet between these sparids was measured using the Bray-Curtis measure (Bray and Curtis 1957). Because sample sizes of predators were unequal, abundance of prey items was standardized as percent numerical abundance for each predator, resulting in values of percent similarity in composition of diet between pairs of

predator species (Clifford and Stephenson 1975; Boesch 1977). Only prey items that were identified to species were included in the similarity analyses. To reduce the data matrix to a size that could be accommodated by the computer program and to eliminate very rare prey species that were not important in the diet of any sparid, only prey species that occurred more than once were included in the analysis.

RESULTS

Whitebone porgy were common in all three depth zones, but they were more abundant at middle and outer shelf stations (5.6 and 5.8 fish per tow, respectively) than on the inner shelf (2.6 fish per tow). Other sparids examined overlapped in depth distribution with whitebone porgy. Sheepshead occurred at inner (1.7 fish per tow) and middle (0.2 per tow) shelf stations. Pinfish (6.2, 1.1, and < 0.1 fish per tow for inner, middle, and outer shelf stations, respectively) and southern porgy (376.8, 562.8, and 0.9 fish per tow) occurred in all three depth zones; red porgy was collected only on the middle (1.4 fish per tow) and outer (5.6 fish per tow) shelf stations.

Whitebone porgy stomachs (N = 219) contained at least 135 species of invertebrates and fishes. Decapods were the most important prey and ranked high in frequency, number, and volume (Table 1). Very small hermit crabs (*Pagurus* spp., *Dardanus* spp., *Paguristes* spp., *Pylopagurus* spp., other Paguroidea) were the dominant decapods in whitebone porgy stomachs, and they sometimes were found along with their gastropod shells, which were usually very damaged. Gastropods were important prey and sipunculids, especially the species *Aspidosiphon gosnoldi* which occupies gastropod shells, were frequently consumed. Gastropods and *Aspidosiphon* sipunculids were often found without their shells. Because mollusk shells were infrequently swallowed by whitebone porgy, many gastropods and pelecypods could not be identified. The gastropod *Costoanachis avara* was the most abundant identifiable mollusk in whitebone porgy stomachs. Other important prey for whitebone porgy included polychaetes, pelecypods, barnacles, and fishes.

TABLE 1.—Percentage of frequency occurrence (F), percentage of number (N), and percentage of volume (V) of prey items and higher taxonomic groups of food in the diet of whitebone porgy, *Calamus leucosteus*.

Taxon Prey item	F	N	V
Algae undetermined	1.3	0.2	<0.1
Porifera undetermined	0.6	0.1	0.2
Cnidaria			
Hydrozoa			
Dynamena sp.	0.6	0.1	<0.1
Halecium sp.	1.3	0.2	<0.1
Total Hydrozoa	1.9	0.2	<0.1
Anthozoa			
Actiniaria undetermined	5.7	0.7	1.5
Athenaria undetermined	8.2	2.4	4.5
Renilla reniformis	1.3	0.2	2.6
Total Anthozoa	15.1	3.3	8.6
Nemertinea undetermined	1.3	0.4	2.0
Annelida			
Polychaeta			
Aglaophamus verrilli	0.6	0.1	<0.1
Ampharete acutifrons	1.3	0.2	<0.1
Amphinomidae undetermined	0.6	0.1	<0.1
Arabella iricolor	0.6	0.1	0.2
Arabella mutans	1.9	0.2	1.0
Arabellidae undetermined	0.6	0.1	0.2
Armandia maculata	0.6	0.2	<0.1
Capitellidae undetermined	0.6	0.1	0.1
Cirratulidae undetermined	1.9	0.2	0.3

Taxon Prey item	F	N	V
Polychaeta—*Con.*			
Diopatra cuprea	1.9	0.2	0.5
Dodecaceria corallii	0.6	0.1	<0.1
Eunice vittata	1.3	0.2	<0.1
Eunicidae undetermined	0.6	0.1	<0.1
Glycera americana	0.6	0.1	<0.1
Glycera sp.	0.6	0.2	0.1
Hydroides crucigera	0.6	0.1	<0.1
Leiochrides pallidior	0.6	0.2	<0.1
Lumbrineris coccinea	0.6	0.1	0.2
Lumbrineris inflata	0.6	0.1	<0.1
Lumbrineris latreilli	0.6	0.1	<0.1
Maldanidae undetermined	5.0	0.7	0.5
Nephtyidae undetermined	2.5	0.3	<0.1
Nephtys incisa	0.6	0.1	<0.1
Nereidae undetermined	0.6	0.1	<0.1
Nichomachinae undetermined	0.6	0.1	0.2
Onuphidae undetermined	1.3	0.2	1.5
Onuphis eremita	2.5	0.4	0.6
Onuphis nebulosa	1.3	0.6	0.4
Onuphis pallidula	0.6	0.1	<0.1
Onuphis sp.	1.3	0.2	<0.1
Opheliidae undetermined	0.6	0.1	<0.1
Paranaitis polynoides	0.6	0.1	<0.1
Petaloproctus socialis	0.6	0.1	<0.1
Phyllodoce longipes	0.6	0.1	<0.1

TABLE 1.—*Continued.*

Taxon Prey item	*F*	*N*	*V*
Annelida—*Con.*			
Polychaeta—*Con.*			
Phyllococe sp.	0.6	0.1	<0.1
Phyllodocidae undetermined	1.3	0.2	<0.1
Polychaeta undetermined	22.6	3.1	1.4
Polydora commensalis	0.6	0.1	<0.1
Psammolyce ctenidophora	0.6	0.1	0.3
Scalibregmidae undetermined	1.3	0.2	0.1
Sigalionidae undetermined	1.3	0.2	<0.1
Spionidae undetermined	0.6	0.1	<0.1
Sthenelais boa	0.6	0.1	<0.1
Sthenelais sp.	1.3	0.2	0.1
Syllidae undetermined	1.3	0.2	0.1
Syllis sp. F	0.6	0.1	<0.1
Terebellidae undetermined	0.6	0.1	0.4
Travisia parva	0.6	0.1	<0.1
Websterinereis sp.	1.3	0.2	<0.1
Total Polychaeta	46.5	9.6	8.6
Mollusca			
Gastropoda			
Buccinidae undetermined	1.3	0.2	0.1
Caecum pulchellum	0.6	0.1	<0.1
Calliostoma baridi	1.9	0.4	0.2
Cerithidea sp.	0.6	0.1	<0.1
Cymatium krebsii	0.6	0.2	<0.1
Costoanachis avara	6.9	2.1	0.2
Costoanachis sp.	0.6	0.1	<0.1
Diodora cayenensis	0.6	0.1	0.5
Epitonium sp.	3.1	2.0	0.4
Epitonium multistriatum	0.6	0.1	<0.1
Fissurellidae undetermined	0.6	0.1	0.2
Gastropoda undetermined	46.5	13.8	7.7
Marginella sp.	1.3	0.2	0.1
Marginella hartleyanum	3.8	1.8	0.9
Marginellidae undetermined	1.9	0.3	0.2
Natica canrena	1.9	0.4	0.2
Naticidae undetermined	4.4	1.1	0.8
Trochidae undetermined	0.6	0.1	<0.1
Total Gastropoda	58.5	23.0	11.4
Pelecypoda			
Americardia media	0.6	0.1	<0.1
Anadara sp.	0.6	0.1	0.7
Brachidontes sp.	0.6	0.1	<0.1
Chione latilirata	1.3	0.2	<0.1
Corbula contracta	3.1	0.5	0.3
Corbula dietziana	0.6	0.2	0.2
Dinocardium robustum	1.9	0.2	0.3
Ervilia concentrica	2.5	0.4	0.3
Glycymeris pectinata	0.6	0.1	<0.1
Laevicardium sp.	0.6	0.2	0.2
Laevicardium laevigatum	3.1	0.5	0.4
Laevicardium pictum	2.5	0.4	0.4
Pectinidae undetermined	1.9	0.2	0.2
Pelecypoda undetermined	11.3	2.0	4.9
Pitar fulminatus	0.6	0.1	<0.1
Pleuromeris tridentata	0.6	0.1	<0.1
Solemya velum	0.6	0.1	0.2

Taxon Prey item	*F*	*N*	*V*
Pelecypoda—*Con.*			
Solenidae undetermined	0.6	0.1	<0.1
Tellina sp.	1.9	0.3	0.1
Total Pelecypoda	21.4	5.6	8.4
Cephalopoda undetermined	0.6	0.1	<0.1
Crustacea			
Ostracoda undetermined	0.6	0.2	<0.1
Copepoda undetermined	0.6	0.1	<0.1
Cirripedia			
Balanoidea undetermined	1.3	0.4	0.5
Balanus sp.	1.9	0.2	<0.1
Balanus trigonus	10.7	5.0	2.6
Balanus venustus	6.3	3.4	1.8
Total Cirripedia	14.5	9.0	5.0
Stomatopoda undetermined	2.5	0.4	0.2
Mysidacea			
Bowmaniella portoricensis	1.9	0.4	<0.1
Mysidae undetermined	0.6	0.1	<0.1
Total Mysidacea	2.5	0.4	<0.1
Cumacea			
Bodotriidae undetermined	0.6	0.1	<0.1
Cyclaspis varians	0.6	0.1	<0.1
Oxyurostylis smithi	4.4	0.7	<0.1
Total Cumacea	5.7	0.8	<0.1
Isopoda			
Apanthura magnifica	0.6	0.1	<0.1
Total Isopoda	0.6	0.1	<0.1
Amphipoda			
Ampelisca sp.	2.5	0.3	<0.1
Ampelisca cristoides	1.3	0.2	<0.1
Ampelisca schellenbergi	0.6	0.1	<0.1
Ampelisca vadorum	1.9	0.3	0.1
Ampelisca venetiensis	0.6	0.2	0.1
Carinobatea carinata	0.6	0.1	<0.1
Caprellidae undetermined	0.6	0.1	<0.1
Corophiidae undetermined	0.6	0.2	<0.1
Elasmopus sp. A	0.6	0.1	<0.1
Erichthonius sp. A	1.3	0.2	<0.1
Erichthonius brasiliensis	2.5	0.3	<0.1
Gammaridea undetermined	3.8	0.6	<0.1
Haustoriidae undetermined	1.9	0.2	<0.1
Lembos smithi	0.6	0.1	<0.1
Lembos spinicarpus inermis	0.6	0.1	<0.1
Lembos unicornis	0.6	0.1	<0.1
Melita appendiculata	0.6	0.1	<0.1
Metharpinia floridanus	1.9	0.4	0.1
Photis sp.	0.6	0.1	<0.1
Phtisica marina	1.9	0.2	<0.1
Podocerus sp. A	0.6	0.1	<0.1
Rhepoxynius epistomus	0.6	0.1	<0.1
Tiron tropakis	0.6	0.1	<0.1
Total Amphipoda	21.4	3.8	0.4

TABLE 1.—*CONTINUED.*

Taxon Prey item	*F*	*N*	*V*
Crustacea—*Con.*			
Decapoda			
Albunea sp	1.3	0.2	0.4
Alpheidae undetermined	1.3	0.3	0.2
Anomura undetermined	0.6	0.2	<0.1
Automate sp.	0.6	0.1	<0.1
Brachyura undetermined	17.0	2.3	3.0
Calappidae undetermined	0.6	0.1	0.1
Callianassa sp.	0.6	0.1	<0.1
Callianassa atlantica	1.3	0.2	0.4
Caridea undetermined	0.6	0.1	<0.1
Dardanus sp.	1.9	0.4	0.1
Diogenidae undetermined	0.6	0.1	<0.1
Dissodactylus mellitae	0.6	0.1	<0.1
Euceramus praelongus	0.6	0.1	0.1
Hepatus epheliticus	1.3	0.2	0.8
Hippidae undetermined	0.6	0.1	<0.1
Hypoconcha arcuata	3.1	0.5	1.3
Iridopagurus dispar	3.1	1.1	0.3
Leptochela sp.	1.9	0.2	<0.1
Leptochela papulata	3.1	1.1	0.4
Majidae undetermined	2.5	0.3	0.4
Mithrax pleuracanthus	0.6	0.1	0.7
Munida irrasa	0.6	0.1	<0.1
Natantia undetermined	5.7	0.7	0.6
Natantia undetermined zoea	0.6	0.1	<0.1
Osachila sp.	0.6	0.2	2.8
Osachila tuberosa	0.6	0.4	0.2
Paguridae undetermined	13.2	2.8	0.7
Paguridea undetermined	8.8	1.2	0.2
Paguristes sp.	1.3	0.2	0.1
Paguristes tortugae	1.3	0.2	<0.1
Pagurus sp.	12.6	3.4	0.8
Pagurus carolinensis	17.0	3.3	0.7
Pagurus hendersoni	17.0	5.1	0.9
Pagurus longicarpus	0.6	0.1	<0.1
Pagurus piercei	2.5	0.3	0.2
Panulirus sp. larvae	0.6	0.1	<0.1
Parthenope sp.	0.6	0.1	0.3
Parthenopidae undetermined	1.3	0.2	0.1
Penaeidae undetermined	0.6	0.2	0.5
Periclimenaeus sp.	0.6	0.1	<0.1
Pilumnus dasypodus	0.6	0.1	<0.1
Pinnixa sp.	0.6	0.1	<0.1
Pinnotheres sp.	0.6	0.1	<0.1
Podochela gracilipes	0.6	0.1	0.1
Portunidae undetermined	2.5	0.3	0.5
Portunus spinicarpus	0.6	0.1	0.1
Pseudomedaeus agassizii	0.6	0.1	0.1
Pylopagurus sp.	0.6	0.1	<0.1
Pylopagurus corallinus	0.6	0.1	<0.1
Pylopagurus discoidalis	0.6	0.1	<0.1
Pylopagurus holthuisi	1.9	0.4	0.1
Synalpheus townsendi	0.6	0.1	0.1
Xanthidae undetermined	1.9	0.2	0.1
Total Decapoda	70.4	27.8	17.3
Crustacea undetermined	1.9	0.2	<0.1
Sipunculida			
Aspidosiphon gosnoldi	17.6	6.2	0.6
Phascolopsis gouldi	1.3	0.2	0.9
Sipunculida undetermined	3.1	0.4	1.5
Sipunculus nudus	0.6	0.1	2.7
Total Sipunculida	22.6	7.0	5.8
Brachiopoda			
Glottidia pyramidata	2.5	0.6	0.1
Total Brachiopoda	2.5	0.6	0.1
Bryozoa			
Antropora tincta	0.6	0.1	<0.1
Bryozoa undetermined	0.6	0.1	<0.1
Diaperoecia floridana	0.6	0.1	<0.1
Hippoporidra janthina	2.5	0.3	0.1
Schizoporella cornuta	3.8	0.4	0.1
Total Bryozoa	6.3	1.0	0.2
Echinodermata			
Asteroidea			
Asteroidea undetermined	0.6	0.1	0.1
Astropecten sp.	3.8	0.4	3.2
Astropecten articulatus	1.9	0.2	1.4
Astropecten duplicatus	1.3	0.3	0.7
Echinaster sp.	1.9	0.3	0.5
Luidia sp.	0.6	0.1	0.5
Luidia alternata	1.9	0.2	2.1
Total Asteroidea	12.0	1.6	8.4
Echinoidea			
Clypeasteroida undetermined	0.6	0.1	<0.1
Echinoidea undetermined	3.1	0.4	1.7
Total Echinoidea	3.8	0.4	1.8
Ophiuroidea undetermined	17.6	2.0	1.2
Holothuroidea			
Holothuroidea undetermined	1.9	0.2	1.4
Thyone sp.	1.3	0.2	4.4
Total Holothuroidea	2.5	0.4	5.8
Chordata			
Ascidiacea undetermined	0.6	0.1	1.8
Pisces			
Bothidae undetermined	0.6	0.1	0.8
Decapterus punctatus	0.6	0.1	0.6
Ogcocephalus parvus	0.6	0.1	1.2
Synodus sp.	0.6	0.1	3.6
Teleostei undetermined	9.4	1.4	6.6
Fish scales	0.6	0.1	<0.1
Total Pisces	12.0	1.8	12.8
Number of stomachs examined	219		
Examined stomachs with food	159		

Whitebone porgy (99–315 mm SL) demonstrated slight changes in feeding habits with increasing size (Table 2). Anthozoans and barnacles (Cirripedia) appeared to be more frequent in the smallest size class, but this may be a result of the small sample of fish < 151 mm SL. Decapods were frequently consumed by all size classes; however, because most decapods eaten were tiny species of hermit crabs, this taxon contributed a much smaller proportion of the prey volume for fish larger than 150 mm SL. Gastropods and sipunculids were also consumed by all size classes. Fishes increased in volumetric importance in the diet of fish up to a length of 250 mm but were not frequently consumed by the largest fish. Echinoderms were more important in the diet of larger whitebone porgy.

Suction and grab samples from the hard bottom stations were dominated by tube-reef building polychaetes, such as *Filograna implexa*, *Phyllochaetopterus socialis*, and *Pista palmata*, as well as epifaunal amphipods (*Erichthonius brasiliensis*, *Luconacia incerta*) that cling to or build tubes on hard substrates or other epibenthic organisms. These species were generally not consumed by whitebone porgy in any

TABLE 2.—Percentage of frequency occurrence (*F*), percentage of number (*N*), and percentage of volume (*V*) of higher taxonomic groups of food in the diet of whitebone porgy, by length interval.

	Length intervals (mm SL)											
	<151			151–200			201–250			>250		
Prey	*F*	*N*	*V*	*F*	*N*	*V*	*F*	*N*	*V*	*F*	*N*	*V*
Algae							3.2	0.3	<0.1			
Porifera										2.3	0.3	0.3
Cnidaria												
Hydrozoa				4.4	0.6	<0.1				2.3	0.3	<0.1
Anthozoa	37.5	9.8	10.0	10.9	4.4	14.8	14.5	2.4	5.8	16.3	2.9	9.2
Nemertinea				2.2	1.1	12.7	1.6	0.2	0.3			
Annelida												
Polychaeta	25.0	9.8	6.9	47.8	9.4	11.6	48.4	8.8	6.8	46.5	11.1	9.3
Mollusca												
Gastropoda	12.5	2.4	0.2	58.7	26.9	16.2	66.1	24.9	11.2	55.8	17.9	10.4
Pelecypoda	12.5	9.8	14.4	21.7	4.2	12.0	22.6	5.8	7.6	20.9	6.4	7.8
Cephalopoda				2.2	0.3	0.1						
Crustacea												
Ostracoda										2.3	0.6	<0.1
Copepoda							1.6	0.2	<0.1			
Cirripedia	37.5	17.1	17.2	8.7	2.5	2.5	14.5	10.4	5.0	16.3	12.3	5.3
Stomatopoda	12.5	2.4	1.0				1.6	0.2	0.2	4.6	0.9	0.2
Mysidacea				8.7	1.7	0.2						
Cumacea				8.7	1.1	0.1	3.2	0.6	<0.1	7.0	0.9	<0.1
Isopoda							1.6	0.2	<0.1			
Amphipoda				17.4	4.2	0.8	29.0	4.3	0.5	18.6	2.9	0.2
Decapoda	50.0	26.8	43.3	71.7	31.7	14.2	71.0	23.0	11.4	72.1	32.8	22.8
Crustacea undetermined				6.5	0.8	0.1						
Sipunculida	12.5	17.1	6.9	23.9	6.7	4.2	33.9	9.5	11.4	7.0	1.5	1.2
Brachiopoda				2.2	0.8	0.2	3.2	0.6	0.1	2.3	0.3	<0.1
Bryozoa							14.5	1.8	0.4	2.3	0.6	0.2
Echinodermata												
Asteroidea				4.4	0.6	5.7	12.9	1.6	7.6	20.9	2.9	10.4
Echinoidea							4.8	0.5	0.4	7.0	0.9	3.6
Ophiuroidea	12.5	2.4	<0.1	15.2	1.9	0.8	21.0	2.1	2.4	16.3	2.0	0.4
Holothuroidea										9.3	1.5	13.1
Chordata												
Ascidiacea										2.3	0.3	4.0
Pisces	12.5	2.4	0.1	8.7	1.1	4.0	19.4	2.7	28.9	4.6	0.6	1.5
Number of stomachs examined		11			62			86			60	
Examined stomachs with food		8			46			62			43	
Mean length of fish with food		125.2			183.7			223.5			272.2	

of the three depth zones (Table 3). Rather, whitebone porgy fed selectively on hard-shelled invertebrate species that were collected only occasionally, or not at all, in suction and grab samples. Many of these prey species are apparently more common in sand bottom habitat (see Discussion).

Whitebone porgy displayed a relatively high similarity in diet to red porgy and sheepshead; overlap in diet with pinfish and southern porgy was low (Table 4).

DISCUSSION

Published information on the diet of *Calamus leucosteus* is lacking. Randall (1967) and Darcy (1986) reported on the food habits of several other Atlantic species of *Calamus* and noted a high incidence of shelled invertebrates such as mollusks, crabs, and echinoids in their diets. Randall (1967) also noted that those *Calamus* spp. which fed on hermit crabs were largely gastropod feeders as well and that sipunculids

TABLE 3.—Relative abundance (percentage of total number of individuals) and electivity values (E) for dominant benthic species in suction and grab samples and in whitebone porgy stomachs. Dominant species include those that ranked in the five most abundant species within stomach or benthic samples in any depth zone for collections pooled for all seasons and years.

	Inner shelf			Middle shelf			Outer shelf		
	Fish stomachs	Benthic samples	E	Fish stomachs	Benthic samples	E	Fish stomachs	Benthic samples	E
Dominant species—benthic samples									
Chone americana	—	0.33	−1.00	—	0.81	−1.00	—	0.59	−1.00
Erichthonius brasiliensis	0.20	2.89	−0.87	0.18	0.30	−0.25	0.66	0.13	−0.66
Erichthonius sp. A	—	0.08	−1.00	—	—	—	0.66	3.75	−0.70
Exogone dispar	—	3.71	−1.00	—	0.47	−1.00	—	0.01	−1.00
Filograna implexa	—	20.42	−1.00	—	63.87	−1.00	—	21.90	−1.00
Luconacia incerta	—	3.27	−1.00	—	1.03	−1.00	—	0.18	−1.00
Malacoceros glutaeus	—	0.41	−1.00	—	0.81	−1.00	—	0.02	−1.00
Phyllochaetopterus socialis	—	0.21	−1.00	—	0.12	−1.00	—	12.40	−1.00
Pista palmata	—	0.09	−1.00	—	0.08	−1.00	—	8.60	−1.00
Podocerus sp. A	—	2.87	−1.00	0.18	0.27	−0.19	—	0.14	−1.00
Spiophanes bombyx	—	0.39	−1.00	—	0.46	−1.00	—	5.81	−1.00
Syllis spongicola	—	2.14	−1.00	—	1.90	−1.00	—	1.38	−1.00
Total	0.20	36.81		0.36	70.12		1.32	54.92	
Dominant species—stomachs									
Costoanachis avara	2.15	0.02	0.98	3.27	<0.01	0.99	—	—	—
Aspidosiphon gosnoldi	12.13	1.63	0.76	3.99	0.46	0.79	0.33	0.09	0.57
Glottidia pyramidata	0.20	0.01	0.88	—	0.01	−1.00	2.31	0.07	0.94
Iridopagurus dispar	—	—	—	0.36	0.01	0.97	4.29	0.07	0.97
Leptochela papulata	—	0.04	−1.00	2.54	0.09	0.93	0.33	0.12	0.46
Marginella hartleyanum	4.70	0.14	0.94	0.18	0.01	0.87	—	0.03	−1.00
Onuphis nebulosa	—	0.01	−1.00	—	0.05	−1.00	2.64	0.56	0.65
Osachila tuberosa	—	<0.01	−1.00	—	<0.01	−1.00	1.98	0.02	0.98
Pagurus carolinensis	2.35	0.40	0.71	4.36	0.30	0.87	2.97	0.07	0.96
Pargurus hendersoni	6.46	0.26	0.92	5.81	0.11	0.96	1.65	0.11	0.88
Total	27.99	2.51		20.51	1.05		16.50	1.14	

TABLE 4.—Percentage of similarity in diet (Bray-Curtis index) between sparid fishes collected from hard bottom habitats.

Species	*C. leucosteus*	*L. rhomboides*	*P. pagrus*	*S. aculeatus*
A. probatocephalus	0.182	0.369	0.125	0.207
C. leucosteus		0.053	0.264	0.060
L. rhomboides			0.037	0.249
P. pagrus				0.076

(*Aspidosiphon* spp.) were occasionally consumed by West Indian *Calamus*. Fishes of the genus *Calamus* have broad molariform teeth (Gregory 1933) that are used to crush the shells of gastropods, hermit crabs, and other invertebrates equipped with hard protective shells, and this is reflected in the food of *C. leucosteus* in the South Atlantic Bight. The motile gastropod shell is apparently a visual stimulus to whitebone porgy, which results in ingestion of the shell regardless of its inhabitant. Gastropods, hermit crabs, and sipunculids that were eaten consisted of very small species. All occupied similarly sized shells, and collumbellid shells (e.g., *Costoanachis avara* and *C. avara* shells occupied by other organisms) were the most frequently found shells in stomach samples.

Whitebone porgy demonstrated a relatively small change in food habits with increasing fish size. This is unusual for sparid fishes, many species of which switch between a herbivorous habit and an omnivorous or carnivorous habit during different life history stages (Christensen 1978; Ogburn 1984; Stoner and Livingston 1984; Darcy 1985a, b; Sedberry 1987). Many of these other sparids occupy grass beds or intertidal waters at certain life history stages and feed on tracheophytes and algae that are common on those shallow-water habitats. Whitebone porgy, like other sparids found in offshore habitats where algae are uncommon, do not feed on plant material (Manooch 1977; Sedberry 1983, 1987).

Most of the invertebrate species that dominated in benthic collections from the hard bottom habitat were not important in the diet of whitebone porgy. Most of these were polychaetes and amphipods that may have been too small to be consumed by a generalized predator like whitebone porgy; however, whitebone porgy probably does not forage directly on hard-bottom reef species, regardless of their size. Dominant prey species such as *Aspidosiphon gosnoldi*, *Glottidia pyramidata*, and *Onuphis nebulosa* are inhabitants of sandy bottoms (Wells and Gray 1964; Cutler 1973; Gardiner 1975; Cooper 1977; Fauchald and Jumars 1979), and *Leptochela papulata* is also commonly found in sandy habitats (Williams 1984).

Calamus leucosteus had a relatively high overlap in diet with *Pagrus pagrus* and *Archosargus probatocephalus*. Pagurid decapods and especially the barnacle *Balanus trigonus* were common in the diet of these three predators but were not consumed by the other sparids examined (South Carolina Wildlife and Marine Resources Department 1984). Aside from a sessile barnacle species, however, few other sessile organisms were consumed by whitebone porgy or red porgy. Red porgy fed mainly on motile decapods and fishes and can be classified as a generalized predator of motile organisms. *Archosargus probatocephalus* appeared to depend more on hard bottom habitat for feeding (Sedberry 1987); whereas, *Calamus leucosteus* fed on a combination of motile invertebrates and fishes, in addition to some hard bottom epifaunal species.

Stenotomus aculeatus had a low overlap in diet with whitebone porgy. Southern porgy, like whitebone porgy, are frequently taken in trawls over sand bottoms (Wenner et al. 1980), but they are not nearly as abundant as they are in hard bottom habitats (Sedberry and Van Dolah 1984). Southern porgy had a diet dominated by a pelecypod (*Ervilia concentrica*) and a cumacean (*Oxyurostylis smithi*) that are infaunal sand dwelling species (Van Engel 1972; Porter 1974); by planktonic species (copepods, *Calanopia americana*, and the caprellid *Phtisica marina*); and by an epifaunal amphipod (*Erichthonius brasiliensis*) that were rarely consumed by whitebone porgy (South Carolina Wildlife and Marine Resources Department 1984; this study). Since these two sparids feed heavily on sand dwelling benthos or near-bottom plankton, they are apparently not dependent on hard bottom habitat for food, although they are found in higher densities in hard bottom areas. Because they feed on different kinds of organisms (infaunal sedentary or planktonic species for southern porgy versus motile epifaunal species for whitebone porgy), there is little overlap in diet between these two species.

Overlap in diet between pinfish and whitebone porgy was very low. Pinfish examined in the present study ate primarily a hard-bottom, sessile, tube-dwelling amphipod, *Erichthonius brasiliensis*, (36% of prey items) that was rarely consumed by whitebone porgy. Pinfish are apparently more closely associated with substrates from which they can browse on attached organisms, as has been noted in previous studies (Stoner and Livingston 1984). Because pinfish fed on attached epifauna, this species was similar in diet to sheepshead, a heavy grazer on attached epifauna (Sedberry 1987). Whereas *Calamus* spp. possess conical teeth in the anterior of the jaws for grasping motile prey and strong molariform teeth on the sides for crushing shells (Gregory 1933; Randall and Caldwell 1966; Randall 1967), the anterior of the jaws of pinfish

are provided with incisors that are suited to scraping epifauna (Stoner and Livingston 1984).

Predation by fishes and other organisms can be an important factor in regulating the structure of sessile invertebrate communities (Peterson 1979; Sedberry 1987); however, it is obvious from the present results that whitebone porgy have little impact on hard-bottom epifaunal communities. While they are an abundant and a dominant member of the predatory fish community (Sedberry and Van Dolah 1984), whitebone porgy do not function as keystone predators (Paine 1969) in hard bottom reefs of the South Atlantic Bight.

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A Photographic Survey of the Megafauna of the Central and Eastern Gulf of Maine

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ABSTRACT: During the summers of 1983 through 1985 the JOHNSON-SEA-LINK manned submersible systems were used to survey the megafauna in the central and eastern Gulf of Maine. Quantitative 35 mm color photographs were taken at 29 stations, 5,714 photos were examined, and the megafauna identified. Eighteen taxa represented 96% of all the organisms counted, and of these 18 only 5 groups, from 2 phyla, were numerically dominant. Ophiuroidea and Asteroidea were the dominant echinoderms while Ceriantharia, *Pennatula*, and *Bolocera* were the dominant cnidarians. The relationship between sediment type and the megafauna was also investigated. Again, relatively few taxa were important and these groups showed substrate specificity. *Pennatula* occurred in a variety of substrates but were most abundant in silt (1.20 individuals m^{-2}). Ceriantharians were generally found in sandy substrates at densities as high as 1.12 m^{-2}, while *Bolocera* dominated on gravel but at much lower densities (0.017 m^{-2}). Scallops, *Placopecten*, were restricted to gravelly sand, while pandalid shrimp occurred on the finer sands and mud, both at low densities ($\leq$0.04 m^{-2}). Asteroidea covered almost the entire range of substrates at low density, although they were more numerous on sands (max. = 0.16 m^{-2}) and gravels (max. = 0.17^{-2}). Ophiuroidea reached their maximum density (1.23 m^{-2}) on slightly gravelly sand but also occurred at $\geq$1 m^{-2} on gravelly mud. The only fish observed at $\geq$0.01 m^{-2} were *Lumpenus lumpretaeformis* and *Merluccius bilinearis*, both of which were found on mud substrates.

The Gulf of Maine has been described as an epicontinental sea or macroestuary extending from Massachusetts to Nova Scotia (Uchupi 1965, 1966; Emery and Uchupi 1972; Campbell 1986). It has its origins in the last glacial period, 11,000 BP (Before Present), having been shaped by both fluvial and glacial erosion (Emery et al. 1965; Ziegler et al. 1965). The resulting uneven topography and mixture of sediments offer a variety of habitats for the establishment of benthic organisms, of both commercial and noncommercial value (Rich 1929; Emery et al. 1965). The distribution and abundance of commercial species have been studied over the years (Bigelow and Schroeder 1939, 1953) but with few exceptions, primarily small-scale studies, the benthic communities have received little attention (Dexter 1944; Stickney 1959; Hanks 1964; Sears and Cooper 1978; Larsen 1979; Hulbert et al. 1982; Larsen et al. 1983a, b; Witman and Cooper 1983). Published reports describing the soft bottom benthos in the offshore regions of the Gulf are limited to the work of Emery et al. (1965), who conducted a geological and biological survey of the U.S. east coast continental shelf, and a study of two contiguous deep basins (Wilkinson and Murray) in the western Gulf by Rowe et al. (1975). Several, as yet unpublished, databases also exist describing the Gulf's benthic communities. One of these is a detailed expansion of the work outlined by Emery et al. (1965) (Theroux and Wigley[1]), while the other is from recent box core sampling and submersible observations in the Gulf (Watling et al. 1988).

The current study was initiated as a submersible survey of offshore lobster habitat in the Gulf of Maine. In addition to this fisheries orientation, however, numerous 35 mm color photographs were taken to characterize the associated megafauna. Because of the paucity of information on the benthic communities of the Gulf, it is the purpose of this paper to summarize the photographic data collected from the years 1983 through 1985 using the JOHNSON-SEA-LINK submersible systems.

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METHODS

During the summers of 1983 through 1985, the JOHNSON-SEA-LINK manned submersible systems were used to survey the megafauna at 29 stations in the Gulf of Maine (Fig. 1; App. Table 1). In 1983, locations in the outer Gulf, Georges Basin and the area northward toward Truxton Swell, were sampled; in 1984, the stations in the middle of the Gulf and Jordan Basin were visited. In 1985, a series of stations running from the center of Jordan Basin to the northeast towards the Bay of Fundy were to be sampled. Unfortunately, weather limited available diving time in 1985 and forced diving operations inshore toward the Nova Scotian coast after only three stations were sampled. The purpose of the study was to document offshore lobster habitat; therefore, dive site selection was based on commercial trap fishery information as well as on National Marine Fisheries Service data from their biannual groundfish trawl surveys of lobster catches.

Submersible dives at each station followed a standard protocol, with the diver-scientist recording observations on a cassette tape or video camera as well as collecting surficial sediment samples over the course of a transect. In addition to these data, 35 mm color photographs were taken automatically at 10 to 15 s intervals throughout the dive.

In the laboratory, a minimum of 200 randomly chose photographs from each dive, or all photos taken during the entire dive if <200 frames total, were individually examined and the megafauna identified and enumerated. The

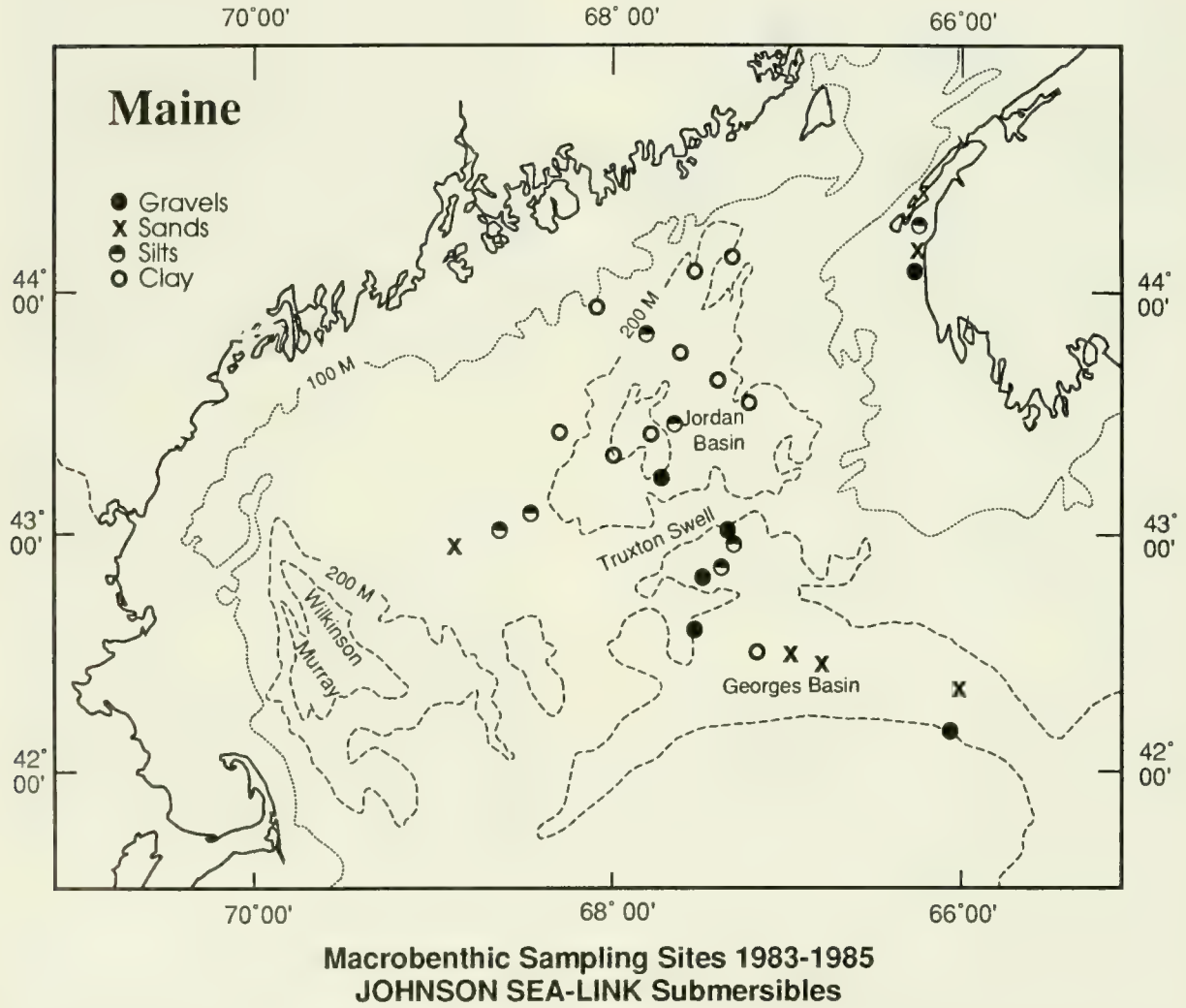

FIGURE 1.—Dive site locations for 29 dives constituting the megafaunal survey, 1983–85, using the JOHNSON-SEA-LINK submersible systems.

categories of megafauna, representing a variety of taxonomic levels, that could be resolved in the photographs are listed in Appendix Table 2. From one to seven sediment samples, collected on each dive, were analyzed by the U.S. Geological Survey for surficial grain size analysis. The statistical parameters for this analysis were calculated by the method of moments (Krumbein and Pettijohn 1938), while the average sediment types for each dive were classified and are described using the terminology of Folk (1980).

RESULTS

Sediment types are shown in Figure 1 at the 29 dive locations. The general sediment pattern, from south to north, is a gradation of coarse to fine sediments. Georges Basin is, generally, sandy along its midsection, changing into a gravelly area towards Truxton Swell. Jordan Basin, which is north of Georges Basin, is dominated by finer silts and clays.

A total of 5,714 color photographs (35 mm slides) were examined from the 29 submersible dives. Over 27,000 individual organisms were counted. The overall taxonomic ranking, based on the percentage of total numbers observed for the top 18 taxonomically distinct groups, is shown in Figure 2. These 18 groups represent 96% of all the organisms counted. From the figure, it is clear that there are only five numerically dominant taxa representing two phyla, the Echinodermata and the Cnidaria. Ophiuroidea and Asteroidea are the dominant echinoderms, while ceriantharian anemones, sea pens of the genus *Pennatula*, and rock (*Bolocera*) anemones account for the dominant cnidarians.

If the same data are examined on a year and location basis, there are, again, very few dominant groups. In addition to the echinoderms and cnidarians observed in all three years, arthropods (pandalid shrimp) were reasonably abundant in 1984 in the middle Gulf and southern Jordan Basin area, while invertebrate tubes (polychaetes or amphipods) occurred at the stations, visited in 1985, in central Jordan Basin and to the northeast (Table 1). The year and area breakdown, like the overall ranking, demonstrates a simple picture for the softer sediment megafaunal communities in the Gulf of Maine. Seven taxonomically distinct groups account for 97 to 99% of all the biota observed.

The relation between sediment type and animal abundance is shown in Figure 3 and detailed in Appendix Table 1. Of interest is the substrate specificity of the various groups. Sea pens, *Pennatula* (most likely *P. aculeata*, Langton, pers. obs.), occurred in clay and silts as well as gravel. They were, however, most common in silt reaching a maximum density of 1.20 animals m^{-2}. They occurred in gravel at only 2 stations compared to 10 stations with

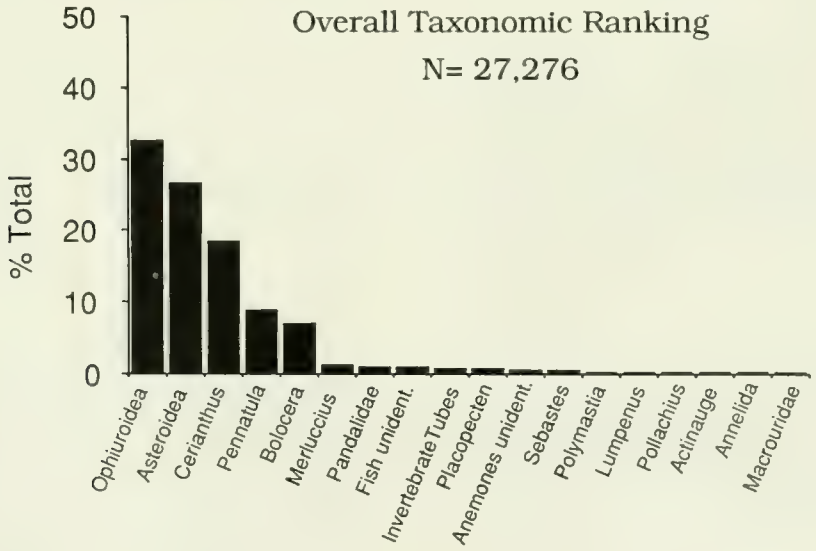

FIGURE 2.—Overall taxonomic ranking, expressed as percentage of the total number of organisms observed (N = 27,276), for 29 submersible dives in the Gulf of Maine from 1983 through 1985.

TABLE 1.—Breakdown of the major groups of benthic organisms, expressed as the percentage of number of total organisms observed, for each of the three years of the survey. These seven groups account for 97 to 99% of all megafaunal animals observed in the areas surveyed for any given year.

Groups	% of major groups by year and location		
	1983 Georges Basin Truxton Swell	1984 Mid-Gulf, Southern Jordan Basin	1985 Central Jordan Basin to the northeast
Pennatula	38.0	28.0	4.0
Cerianthus	38.3	5.0	10.3
Bolocera	10.1	–	1.3
Invertebrate tubes (Polychaete or Amphipod)	–	–	2.1
Pandalidae	–	1.2	–
Asteroidea	6.5	2.5	11.5
Ophiuroidea	2.8	62.2	67.9
Total %	97.5	98.9	97.1

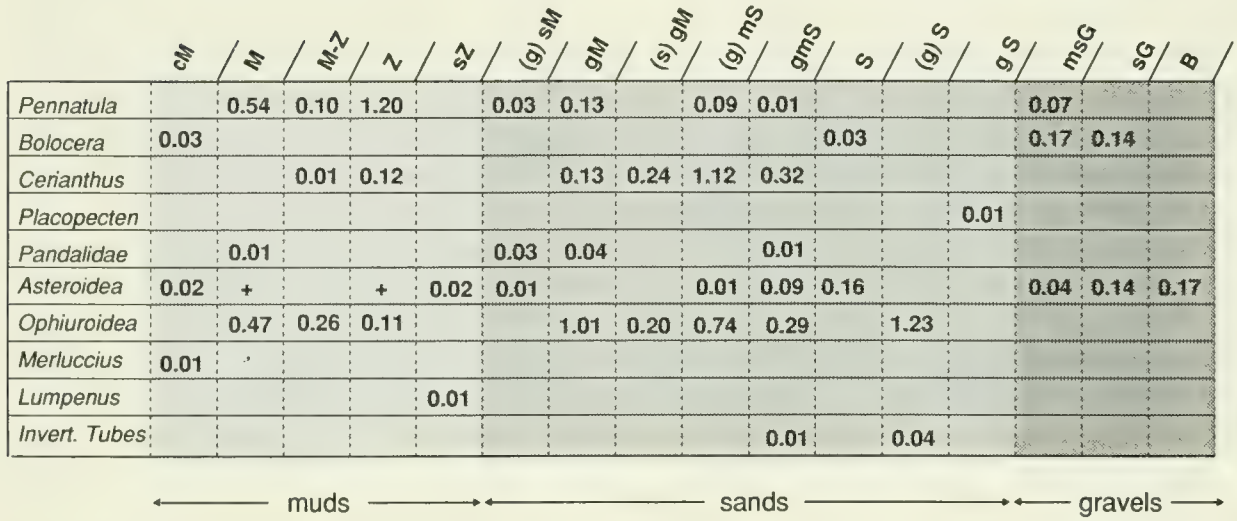

FIGURE 3.—Occurrence of dominant megafaunal groups associated with substrate type. Data is expressed as numbers of individuals per square meter of bottom for each sediment type. Only taxa that had a density of ≥0.01 animals per squre meter in any one sediment type are included in the figure. The actual density is given when it equals or exceeds the 0.01 value while a "+" indicates presence but at a density of <0.01 animal per square meter. The sediment types follow the terminology of Folk (1980) and are cM = clayey mud, M = mud, M-Z = Mud-Silt, Z = Silt, sZ = sandy silt, (g)sM = slightly gravelly sandy mud, gM = gravelly mud, (s)gM = slightly sandy gravelly mud, (g)mS = slightly gravelly muddy sand, gmS = gravelly muddy sand, S = sand, (g)S = slightly gravelly sand, gS = gravelly sand, msG = muddy sandy gravel, sG = sandy gravel, and B = boulder field.

clay and silt substrates. *Cerianthus* sp. (probably *C. borealis*, see Shepard et al. 1986), a burrowing anemone, was also not especially substrate specific. It was found over the entire gradation of sandy substrates as well as some of the silts, although it reached its highest density (1.12 m^{-2}) in slightly gravelly muddy sand. *Bolocera tuediae*, on the other hand, is an anemone that attaches to hard, rocky, substrates. Consequently, it was observed in areas of gravel and sand at a maximum density of 0.17 m^{-2}. On the sandy substrates, these anemones, as well as the few animals observed on clayey mud, were often found attached to a rock outcrop or loose boulder rather than directly to the finer sediment. The sea scallop, *Placopecten magellanicus*, was restricted to gravelly sand while pandalid shrimp occurred on finer sands and muds; both at relatively low densities, 0.01 and ≤0.04 m^{-2}, respectively. Asteroidea which include a variety of genera (e.g., *Asterias*, *Hippasteria*, *Henricia*, *Cros-*

saster, and *Solaster*) occurred over virtually all substrate types but were more prevalent on coarser sediments, reaching a maximum density of 0.17 m^{-2} in a bouldery area. In contrast, Ophiuroidea did not occur on gravel substrates in significant numbers but did occur on slightly gravelly sand at high density (1.23 m^{-2}) as well as on the finer sands and muds. Only two fish species occurred in sufficient density to demonstrate any substrate specificity. The silver hake, *Merluccius bilinearis*, was observed resting on the bottom on fine mud sediments, while the snake blenny, *Lumpenus lumpretaeformis*, was observed on sandy silt.

DISCUSSION

This study is the first, broad scale, megafaunal survey in the Gulf of Maine using manned submersibles. Previous submersible work was limited to four DSRV *Alvin* dives in Wilkinson and Murray Basins in 1971 and 1972, described by Rowe et al. (1975). The study by Rowe et al. reported that pandalid shrimp and ophiuroids were the numerically dominant megafaunal animals observed along several transects in these basins. From the present work, it is clear that ophiuroids are numerically dominant throughout the central and eastern Gulf on the finer sediments (Figs. 2, 3). Pandalid shrimp, on the other hand, ranked only seventh in abundance in the present work (Fig. 2). Perhaps the abundance of shrimp observed by Rowe et al. (1975) reflected the high population levels, and correspondingly high catches, of *Pandalus borealis* that occurred in the Gulf of Maine in the late 1960s and early 1970s (Shumway et al. 1985).

The description of the megafauna in the Gulf of Maine that emerges from this study is not complex. Relatively few taxa, or taxonomic groups, from two phyla dominated the megabenthos on a numerical basis (Fig. 2; App. Table 1). These two phyla (Echinodermata and Cnidaria) are different from the dominants identified from macrobenthic surveys in the Gulf, as might be expected, owing to the methodological differences and scales of resolution. Theroux and Wigley (fn. 1), for example, reported molluscs, annelids, and crustaceans to be the numerical dominants, based on a more extensive and geographically restricted analysis of the Emery et al. (1965) survey, using surface deployed sampling gear. Watling et al. (1988) identified annelids, crustaceans, and echinoderms as the numerically dominant groups based primarily on surface deployed box core samples. Neither ceriantharians nor pennatulids, the numerical dominants in this study, are adequately sampled with a 0.1 m^2 box core (Watling[2]). Rowe et al. (1975) also noted significant differences between core samples and visual counts, while other studies specifically comparing submersibles and photographic transects with other sampling gear have shown substantial differences when conducting a faunal census (Wigley and Theroux 1970; Uzmann et al. 1977; Theroux 1984).

The distribution of megafaunal animals is related to sediment type in the Gulf of Maine (see Figure 3 and Appendix Table 1). Watling et al. (1988) also identified substrate, together with the temperature range of the overlying water mass, as major factors resulting in seven discrete macrobenthic species assemblages in the Gulf of Maine. Their analysis is based on both box core and submersible sampling. Zoogeographic studies on specific megafaunal components in the Gulf of Maine are rare, only three taxonomic groups occurring in this geographic region have been investigated (Wigley 1960; Haynes and Wigley 1969; Franz et al. 1981; Shepard et al. 1986). In these three instances the various environmental factors, including sediment type, that potentially control the animals distributional patterns have been examined. Shepard et al. (1986), for example, completed an extensive study of Ceriantharia off the northeast coast of the United States. Geographic and bathymetric zonation was attributed primarily to temperature and secondarily to food supply and sediment type. They found *Cerianthus* to be tolerant of a wide range of temperature (8°–16°C) and to occur on most substrates except gravel and coarse shifting sand. In the present study ceriantharians were also found to have little substrate fidelity although there was a noticeable absence from areas of boulders and gravel (Fig. 3). Pandalid shrimp, on the other hand, have been shown to have a stronger affinity for sediment type (Wigley 1960). Unfortunately the species of shrimp could not be identified in the photographs we examined so a detailed comparison with Wigley's results on the four species of Pandalidae occurring in the Gulf of Maine is not possible. Nevertheless, Haynes and Wigley

[2]L. Watling, Darling Marine Center, University of Maine, Walpole, ME 04573, pers. commun. 1988.

(1969), as well as Bigelow and Schroeder (1939) in an earlier study, have both noted a strong affinity between organically rich sediment and the occurrence of the Gulf's largest pandalid, *Pandalus borealis*. The observed occurrence of shrimp in our photographs corresponds to substrates containing silt and, generally, finer grained materials (Fig. 3), thus, once again, confirming the relationship between pandalid shrimp and, presumably, high organic sediments in the Gulf of Maine. In the last of the three groups, for which there is information relating distributional patterns to the environment, Franz et al. (1981) identified temperature as the major controlling factor of asteroid distribution. Their study identified 15 different species of seastar in the Gulf of Maine which they assigned to 3 zoogeographic groups. These species have a variety of substrate requirements. In our study temperature varied little between dive locations, depth, and year (App. Table 1), whereas sediment type did. This variation in substrate is reflected in Figure 3 where asteroids are shown to occur on almost all sediment types. Although sediment type is obviously not the only factor that determines a species occurrence, it is important when considering the patterns of species distribution throughout the Gulf of Maine and should be evaluated on a species specific level.

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APPENDIX TABLE 1.—Summary of data for 29 submersible dives conducted using the JOHNSON-SEA-LINK submersible systems from 1983—85 in the Gulf of Maine. Mean percentage of sediment composition categories: G = gravel; SA = sand; SI = silt; CL = clay. "Most abundant animals" includes any group where 10 or more individuals were counted in the photographs from each dive.

Date (Mo/day)	JSL I or II Dive #	Dive location Lat. N	Dive location Long. W	Max. depth (m)	Bottom temp. (°C)	Sediment $\bar{x}$% composition G SA SI CL	No. of sediment samples	Most abundant animals (#m $^{-2}$)
1983								
8/3	1407	42°58.48′	67°31.18′	226	8.8	0/46/35/19	1	0.024 *Bolocera* 0.023 Asteroidea 0.005 *Merluccius* 0.004 Fish unid.
8/3	1408	42°58.48′	67°31.18′	229	8.7	0/33/44/23	1	0.030 *Bolocera* 0.013 Asteroidea 0.012 *Merluccius*
8/4	1409	43°01.30′	67°32.12′	201	8.8	38/45/12/5	4	0.214 *Pennatula* 0.044 *Bolocera* 0.028 Asteroidea
8/4	1410	43°04.12′	67°43.24′	153	8.2	36/50/10/4	3	0.115 *Bolocera* 0.047 Asteroidea 0.008 *Polymastia*
8/5	1413	42°45.18′	67°37.30′	206	8.9	44/45/8/3	5	0.346 *Bolocera* 0.043 Asteroidea 0.021 *Pollachius*
8/6	1414	42°28.18′	67°20.06′	323	8.7	0/5/64/31	2	2.408 *Pennatula* 0.243 *Cerianthus* 0.008 Macrouridae 0.007 Asteroidea
8/6	1415	42°26.24′	67°07.36′	381	8.6	5/41/37/17	5	0.238 *Cerianthus* 0.204 Ophiuroidea
8/7	1416	42°08.30′	66°09.00′	177	8.1	61/38/<1/<1	4	0.085 *Bolocera* 0.013 Asteroidea
8/8	1418	42°14.30′	66°09.00′	264	7.3	10/89/<1/<1	7	0.010 *Placopecten*
8/8	1419	42°23.42′	66°52.48′	351	7.9	4/52/26/18	5	2.234 *Cerianthus* 0.179 *Pennatula* 0.010 Asteroidea
8/10	1422	42°32.00′	67°38.00′	171	8.7	38/53/<1/2	5	0.254 Asteroidea 0.201 *Bolocera*
1984								
7/17	880	42°51.31′	68°54.04′	144	6.9	13/68/13/6	2	0.327 *Cerianthus* 0.182 Asteroidea 0.009 *Sebastes*
7/18	881	42°58.11′	68°44.25′	205	7.3	3/32/39/26	3	0.034 Pandalidae 0.032 *Pennatula* 0.010 Asteroidea
7/18	882	43°03.16′	68°32.43′	181	7.0	7/29/39/25	3	1.009 Ophiuroidea 0.126 *Pennatula* 0.125 *Cerianthus* 0.039 Pandalidae

APPENDIX TABLE 1.—*Continued.*

Date (Mo/day)	JSL I or II Dive #	Dive location Lat. N	Dive location Long. W	Max. depth (m)	Bottom temp. (°C)	Sediment $\bar{x}$% composition G SA SI CL	No. of sediment samples	Most abundant animals (#m^{-2})
1984—*Continued*								
7/19	883	43°48.31′	67°54.22′	174	7.3	0/<1/64/36	1	2.418 *Pennatula* 0.021 *Merluccius* 0.017 Pandalidae
7/19	885	43°20.55′	68°24.46′	194	7.8	0/<1/56/44	3	0.973 Ophiuroidea 0.302 *Pennatula* 0.009 Pandalidae
7/20	887	43°17.45′	67°55.44′	231	7.9	0/<1/57/43	3	0.594 Ophiuroidea 0.116 *Pennatula* 0.012 Pandalidae
7/20	888	43°22.32′	67°43.52′	270	8.1	0/<1/58/42	3	0.555 Ophiuroidea 0.214 *Pennatula*
7/21	889	43°54.01′	68°05.32′	180	7.4	0/<1/60/40	2	0.603 *Pennatula* 0.025 Asteroidea
7/21	890	43°43.01′	67°43.06′	236	9.2	0/<1/56/44	2	1.183 Ophiuroidea 0.019 Invert. tubes
7/21	891	43°37.26′	67°31.29′	227	8.3	0/<1/69/31	2	0.221 Ophiuroidea
7/22	892	43°27.19′	67°31.48′	224	8.0	3/19/53/26	2	1.472 Ophiuroidea
7/22	893	43°30.27′	67°18.35′	220	9.2	0/7/59/34	2	0.123 *Pennatula*
1985								
6/25	1093	43°58.14′	67°26.52′	187	7.9	15/37/36/12	3	0.584 Ophiuroidea 0.304 *Cerianthus* 0.027 Invert. tubes 0.021 *Pennatula* 0.011 Pandalidae
6/25	1094	44°04.22′	67°35.45′	201	8.2	0/2/65/32	1	0.260 Ophiuroidea 0.096 *Pennatula* 0.009 *Cerianthus*
6/26	1095	44°08.13′	67°26.52′	242	8.9	1/7/61/31	4	1.225 Ophiuroidea 0.037 Invert. tubes
6/27	1096	44°16.13′	66°16.47′	52	9.1	0/39/55/6	1	0.021 Asteroidea 0.011 *Lumpenus*
6/27	1097	44°09.52′	66°13.37′	23	8.7	<1/97/2/<1	1	0.156 Asteroidea 0.026 *Bolocera*
6/28	1098	44°03.28′	66°13.57′	18	9.6	boulders	—	0.169 Asteroidea

APPENDIX TABLE 2.—Listing of the categories of megafauna that could be resolved and identified in the 35 mm photographs. The actual area of sea floor photographed in each frame was 7.0 m^2.

Macrophytes	Echinodermata
Porifera	Echinoidea
Orange colonial forms	*Echinarachnius parma*
White colonial forms	Asteroidea
Yellow colonial forms	Ophiuroidea
Stalked sponges	Vertebrata
Sponge, unidentified	*Myxine glutinosa*
Polymastia	*Omochelys cruentifer*
Cnidaria	*Merluccius bilinearis*
Hydroids	*Gadus morhua*
Tubularia	*Melanogrammus aeglefinus*
Pennatula	*Pollachius virens*
Bolocera	*Urophycis* sp.
Actinauge	*Brosme brosme*
Cerianthus	Macrouridae
Anemones, unidentified	Flatfish
Brachiopoda	*Sebaster fasciatus*
Mollusca	*Myoxocephalus* sp.
Gastropoda (Welks)	*Aspidophoroides monopterygius*
Placopecten magellanicus	*Lumpenus lumpretaeformis*
Annelida	Blenny, unidentified
Invertebrate tubes	*Leptoclinus maculatus*
(Polychaete or Amphipod)	*Macrozoarces americanus*
Arthropoda	*Lophius americanus*
Pandalidae	Fish, unidentified
Homarus americanus	
Pagarus sp.	
Cancer sp.	

Submersible Observations of Deep-Reef Fishes of Heceta Bank, Oregon

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W. H. Barss, and R. M. Starr

ABSTRACT: Rockfishes, *Sebastes* spp., were the most numerous and speciose fishes seen during 16 submersible dives from 64 to 305 m depth in the vicinity of Heceta Bank off the coast of Oregon. Dense schools of juvenile rockfishes and large yellowtail rockfish, *S. flavidus*, were observed only over rocky, high relief areas near the top of the bank, and highest densities of small benthic rockfishes (up to 5–10/m^2) on the flanks of the bank. These observations suggest that shallow, rocky portions of Heceta Bank are a nursery area for juvenile rockfishes. Two species groups of nonschooling fishes were identified based on transects over the diverse seafloor habitats around the bank: one comprised primarily of rockfishes in shallow water on rock and cobble, and the other comprised of flatfishes, agonids, sablefish, and some rockfishes in deep water over mud and cobble. Species composition of fishes observed from submersible dives differed from species composition of fishes taken from trawl catches in the same general areas.

Prominent offshore submarine banks of exposed bedrock, formed by subduction of oceanic plates, occur along the continental shelf of western North America (Kulm and Fowler 1974), providing a specialized habitat for marine fauna. Large aggregations of rockfishes (Scorpaenidae: *Sebastes*) and other fishes are often associated with these banks (Isaacs and Schwartzlose 1965), just as concentrations of fishes are found on or over seamounts in the North Pacific Ocean (Uda and Ishino 1958; Uchida and Tagami 1985; Uchida et al. 1986).

Heceta Bank, located about 55 km off the central Oregon coast, rises abruptly from depths of over 1,000 m on its seaward face to depths of <60 m (Figs. 1, 2). Trawlable areas around Heceta Bank support a large portion of Oregon's commercial fishery production. The bank itself is thought to be a nursery for juvenile fishes. Several surveys of near-bottom fishery resources of the region have been attempted using bottom trawls (Gunderson and Sample 1980; Barss et al. 1982; Weinberg et al. 1984). However much of the bank is too rugged for bottom trawling, and until our study, no submersible surveys of this area had been made. Thus, species composition, abundances, and distributions of fishes on Heceta Bank itself are largely unknown.

We used a manned submersible to conduct surveys of fishes on and around Heceta Bank. Our goals were to assess visually the abundances of fishes on Heceta Bank, to relate distributions and species assemblages with habitat type and depth, and to evaluate the importance of the bank as a nursery and refugium for commercially important fishes.

METHODS

We dove 16 times in the vicinity of Heceta Bank (Fig. 2) during daylight on 23–31 August 1987, using the submersible *Mermaid II*. Bottom depths ranged from 64 to 305 m. Usually two or three visual belt transects were made during each dive. During each transect the position of the submersible and the distance traversed in 30 minutes at speeds of 1.5–2.0 km/h were determined from Loran C fixes by the surface vessel *Aloha* as it followed a surface buoy towed by the submersible. In this paper we report on 21 transects from 10 dives in which the submersible attempted to follow a compass course parallel to isobaths. Two scientists and a pilot were on each dive. Scientists switched positions from the bow window to a stern jump seat between 30 min transects. Seven scientists made dives.

All fishes seen between two fixed points on the submersible's bumper (a path about 3.5 m wide

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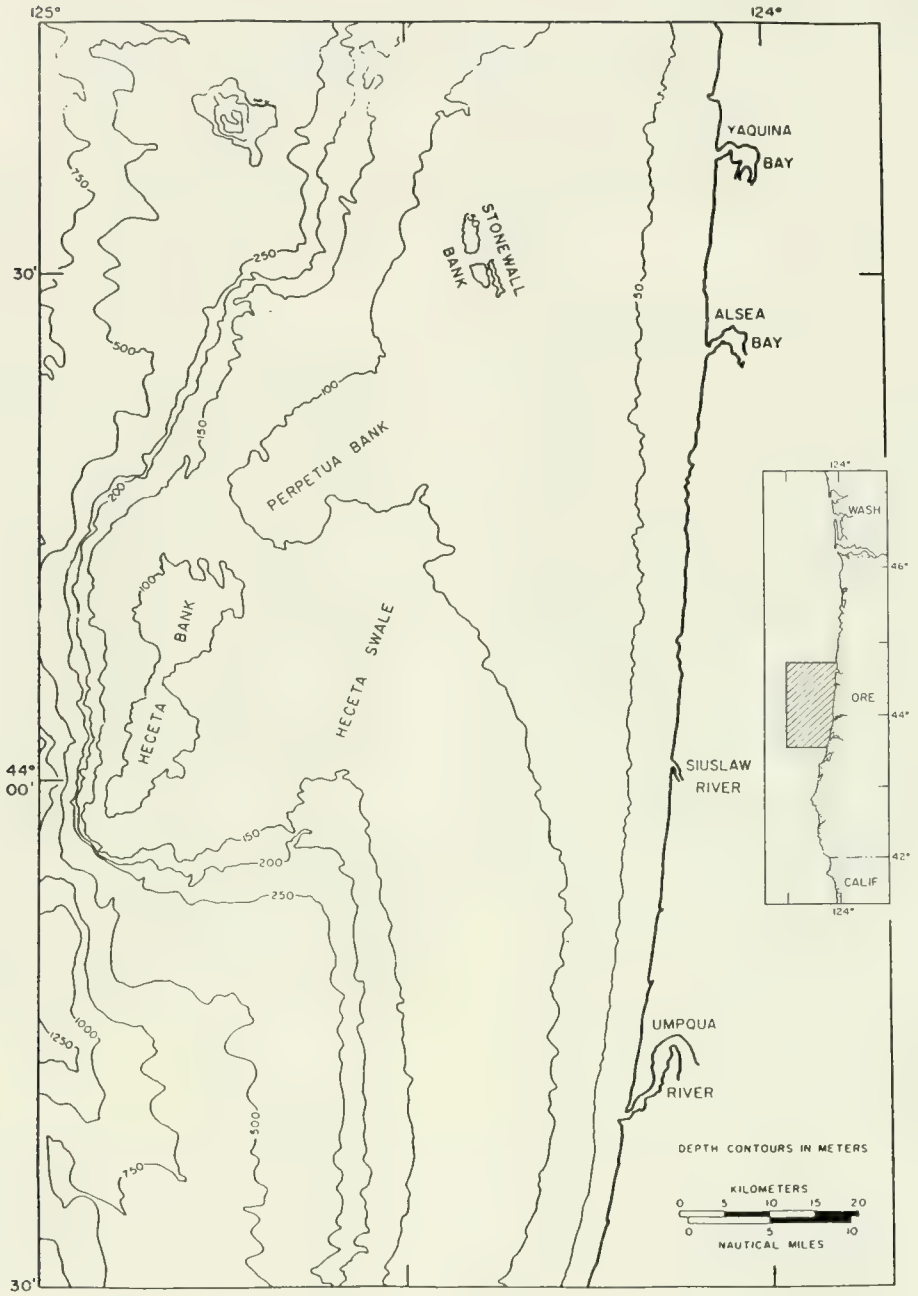

FIGURE 1.—Chart of the central Oregon coast showing Heceta Bank (depth in meters), and insert showing area covered by chart.

on the bottom at an altitude of 2 m) were identified when possible, counted, and lengths estimated to the nearest 10 cm. These data were simultaneously recorded on tape recorders and/or an event recorder by one of the two scientists on each dive. Altitude above the bottom was determined by observing a length of chain marked in decimeters suspended below the submersible and visible from the port. Altitude was fairly constant, about 2 m, on dives over uniform bottom. A fiberglass "T"-shaped rod, protruding 2.5 m from the bow of the submersible with black and white bands at 10 cm intervals, and a similar 50 cm bar with 10 cm bands attached to the bottom of the chain were used to estimate fish lengths.

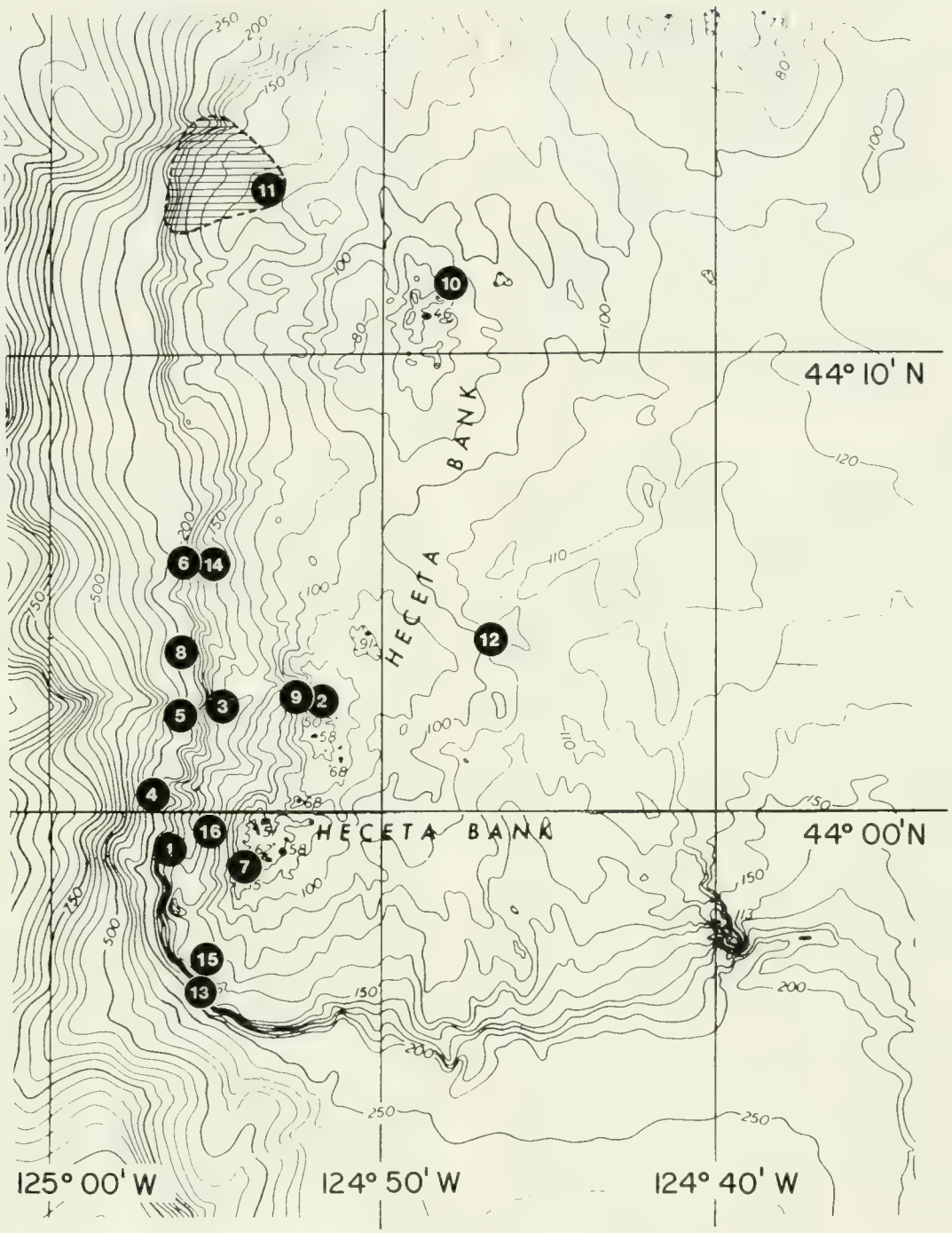

FIGURE 2.—Location of the 16 dives on Heceta Bank. Hatched areas indicate locations of bottom trawling.

External lighting consisted of two 500 W and two 150 W iodide lamps. A Photo-Sea 1000[1] 35 mm camera with strobe and a CM-55 Underwater Television Camera were used on every dive to assist in identification of fishes after the dives. We used a slurp gun and rotenone dispenser (Straty 1987) to collect voucher specimens. Between transects on some dives the submersible rested on the bottom with lights and

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

thrusters off for about 10 minutes. The lights were then turned on to determine their effects on fish behavior. Although "marine snow" was sometimes dense, visibility near the bottom was 3–5 m on all dives. Observations were sometimes made with ambient light from the submersible's conning tower at shallow depths.

A hierarchical cluster analysis (see Pimentel 1979), using presence or absence of species, was used to determine the similarity of nonschooling fish assemblages among transects. Schooling fishes were not included because most were small and could not be accurately enumerated or identified to species.

RESULTS

We encountered diverse and patchy substrates. Bottom types ranged from soft mud to rock walls and pinnacles. The bottom was often mud at depths below about 150 m, and cobble or rock at shallower depths. Massive rock formations, often sculptured into ridges and valleys, existed at depths of 75 m or less. Although habitats were generally stratified by depth, bottom type typically varied within a dive.

We observed a total of 42 taxa of fishes, including 31 identified species (Table 1). Rockfishes (Scorpaenidae) were by far the most abundant and speciose group: 12 species of *Sebastes* were identified. Of the nonschooling fishes, small "blotched" rockfishes, tentatively identified as sharpchin rockfish, *S. zacentrus*, were seen more frequently on transects of contour dives than all other fishes combined (Table 1). Rockfishes ranked first in abundance on 15 transects and second in abundance on 10 of the 21 transects (Table 2). The most numerous of the identified nonschooling species was the rosethorn rockfish, *Sebastes helvomaculatus*. The most numerous of the identified schooling species was yellowtail rockfish, *S. flavidus*; sometimes nonschooling individuals of this species were seen.

TABLE 1.—Rank order of abundances of nonschooling fishes seen on the 21 transects on Heceta Bank.

Nonschooling fishes	Total no. observed
Sharpchin rockfish, *Sebastes zacentrus?*	949
Unidentified small rockfish	902
Rosethorn rockfish, *Sebastes helvomaculatus*	409
Zoarcidae	164
Sablefish, *Anoplopoma fimbria*	140
Pygmy rockfish, *Sebastes wilsoni?*	132
Slender sole, *Lyopsetta exilis*	99
Dover sole, *Microstomus pacificus*	97
Unidentified large rockfish	71
Agonidae	67
Greenstriped rockfish, *Sebastes elongatus*	55
Unidentified flatfish	52
Cottidae	51
Hagfish	40
Shortspine thornyhead, *Sebastolobus alascanus*	33
Slim sculpin, *Radulinus asprellus*	33
Rex sole, *Glyptocephalus zachirus*	33
Splitnose rockfish, *Sebastes diploproa*	32
Yelloweye rockfish, *Sebastes ruberrimus*	25
Canary rockfish, *Sebastes pinniger*	25
Kelp greenling, *Hexagrammos decagrammus*	23
Unknown fish	21
Darkblotched rockfish, *Sebastes crameri*	19
Yellowtail rockfish, *Sebastes flavidus*	16
Lingcod, *Ophiodon elongatus*	14
Spotted ratfish, *Hydrolagus colliei*	12
Longnose skate, *Raja rhina*	10
Blenniidae	8
Bathymasteridae	8
Rajidae	7
English sole, *Parophrys vetulus*	7
Redbanded rockfish, *Sebastes babcocki*	7
Arrowtooth flounder, *Atheresthes stomias*	6
Big skate, *Raja binoculata*	4
Pacific hake, *Merluccius productus*	4
Tiger rockfish, *Sebastes nigrocinctus*	2
Wolf-eel, *Anarrhichthys ocellatus*	2
Sand sole, *Psettichthys melanostictus*	2
Stripetail rockfish, *Sebastes saxicola*	1
Ragfish, *Icosteus aenigmaticus*	1
Sand dab, *Citharichthys* sp.	1
Threadfin sculpin, *Icelinus filamentosus*	1
Osmeridae	1
Greenspotted rockfish, *Sebastes chlorostictus*	1

Assemblages of Nonschooling Fishes

Cluster analysis grouped the nonschooling fishes into two major groups associated with two major habitat types and two depth zones—bottoms where rock and cobble predominated at depths of 67–145 m (Habitat I:13 transects) and mud and cobble bottoms at depths of 140–299 m (Habitat II:8 transects) (Fig. 3, Table 2). Two subclusters occurred within each habitat group at a Euclidian distance of <0.4. The distance (dissimilarity) between the two major habitat types was almost twice as great as among the four subclusters. As can be seen in Table 2, differences in species compositions among clusters were not large. Many species were found in several habitat/depth types. Distinct species assemblages were not obvious. The four habitat groups were as follows:

IA-Shallow Rock Habitat. Six transects near the top of the bank (67–76 m) were over a seafloor predominated by high-relief, massive rock walls often separated by eroded valleys filled with cobble or sand. Four transects were over cobble and flat rock interspersed with patches of mud at depths of 104–149 m. Crinoids (*Florometra serratissima*), sponges, anemones (*Metridium* sp.), hydrocorals, and bryozoans were abundant on exposed rock faces. Basket stars (*Gorgonocephalus* sp.) were obvious on ridge tops. Rockfishes were the most frequently observed fishes, especially rosethorn, small sharpchin rockfishes, and large yelloweye (*S. ruberrimus*), and yellowtail rockfishes.

IB-Shallow Cobble Habitat. Three of the transects were at 122–145 m over cobble and lower relief rocks interspersed with soft sediments on the northern portion of the bank (Fig. 1). Rosethorn, yelloweye, canary (*S. pinniger*), and large sharpchin rockfishes occurred near rocks, and zoarcids and longnose skates (*Raja rhina*) were seen in muddier areas.

IIA-Deep Mud-Cobble Habitat. Two of the transects were over mud and cobble substrates in deeper water (185–220 m and 140–148 m, respectively). Rosethorn, greenstriped (*S. elongatus*), canary, and yellowtail rockfishes occurred in these two transects but were absent in deeper transects over mud bottoms. However, the fishes seen on these transects were similar to mud bottom assemblages because of the occurrence of several species of flatfishes. Greenstriped rockfish and Dover sole, *Microstomus pacificus*, occupied soft bottom areas between rocks.

IIB-Deep Mud Habitat. Six transects were over mud, which was the predominant substrate at the deepest depths, 164–300 m, although occasional small rock outcrops or boulders were evident there. Sea urchins, *Allocentrotus fragilis*; sea stars, *Pycnopodia helianthoides*; sea cucumbers, *Parastichopus californicus*; and crabs *Lopholithodes foraminatus* were common in this habitat. All these invertebrates had very patchy distributions. We saw zoarcids, Dover sole, and unidentified flatfishes on all six of these transects, and hagfish (*Eptatretus* sp.); rex sole, *Glyptocephalus zachirus*; slender sole, *Lyopsetta exilis*; sablefish, *Anoplopoma fimbria*; poachers (Agonidae); and skates (Rajidae) on most transects. The deep mud habitat included some species also seen over shallow rock and cobble as well as species only observed over deep mud and cobble (Table 2).

The two cobble subgroups (IB and IIA) are probably transitional habitats between shallow rock (IA) and deep mud (IIB). As such they allow comparisons of the occurrence of fishes on similar bottom types at different depths. Yelloweye and canary rockfish appeared to be more common at shallow than deep cobble, whereas splitnose and greenstriped rockfish, cottids, Dover sole, and other flatfishes were more frequently seen over deep than over shallow cobble. Rosethorn rockfish were common in both subgroups (Table 2).

Six to 22 different species of nonschooling fishes were identified on individual transects. Interestingly, the fewest species of fishes (6–12) were seen on the shallowest dives, over rocky and cobble bottoms (67–149 m; Habitat I), while the greatest number (10–22) were seen on deeper dives over mud and cobble bottoms (164–299 m; Habitat II) (Table 2; Mann-Whitney U–test, $P < 0.01$). This difference would be reduced if the unidentified schooling rockfishes seen in shallow water (see below) could have been included. Average density of nonschooling fishes observed varied greatly (0.02–1.3/m^2) within and among habitat types. No difference was found in the densities between Habitat I and Habitat II (Mann-Whitney U-test, $P > 0.2$). Fish density was highest on dives over slabs of flat rock at 149 m (15A) where large numbers of juvenile rockfishes were seen.

Rockfishes

Because rockfishes were the most numerous and diverse family of fishes seen on our dives (Tables 1, 2) and because they are taxonomically a cohesive group with distinct behavioral patterns, they merit special consideration. Most individuals could be categorized into one of four distinct size groups and behavior patterns: 1) schools of small or juvenile fishes, 2) solitary benthic fishes of intermediate size, 3) pelagic schools of large fishes, and 4) large solitary rockfish near the bottom.

Small Schooling Rockfishes

We saw 24 schools, comprised of 10 to several thousand small (<10 cm) unidentified reddish juvenile rockfishes, during 5 of the 16 dives.

TABLE 2.—Number of nonschooling fishes observed on 21 transects on Heceta Bank, groupings and Table 1 for scientific names. (Because transect lengths

	I: Shallow rock and cobble												
Habitat:	IA: Rock										IB: Cobble		
Depth (m):	67-85	67-85	67-85	72-76	72-76	72-76	104-107	104-107	149	149	145	122-145	122-145
Species / Drive-transect:	2A	2B	2C	9A	9B	9C	12A	12B	15A	15B	11B	11C	11A
Rosethorn RF	25	5	2	37	16	44	24	31	31	12	37	12	28
Yelloweye RF	6				1	3			1		5	3	3
Lingcod	5			1	1	4	1					1	
Small RF	3	2		7		11	12	3	825	30	1	1	
Pigmey RF									126				
Ratfish	2						4						
Sanddab	1												
Cottidae		12	6	3			4	10			1		
Greenstriped RF		3	8				15	4		2			1
Zoarcidae		2	1	19	1		1				2	5	4
Canary RF		2		2					1		3	2	7
Yellowtail RF		2		2	5	5							
Kelp greenling	8	2		1	6	3					1	1	
Wolf-eel		1											
Large RF						2	1	2	4	3	21	5	
Longnose skate						1			1		1	1	1
Sharpchin RF							3	2	751	85	4	6	9
Hagfish							3	4	3				1
Dover sole			1				7	3	1	2			
Redbanded RF									1				
Darkblotched RF				7								4	
Splitnose RF				1							3		
Tiger RF				1								1	
Big skate			1										2
Bathymasteridae								8					
Blenniidae							8						
Stripetail RF											1		
Agonidae												1	
Rajidae													3
Rex sole													1
Flatfish													
Thornyhead													
Arrowtooth Fl													
English sole													
Slender sole													
Pacific hake													
Sablefish													
Ragfish													
Sand sole													
No. fish types	7	9	6	11	6	8	12	9	11	6	12	13	11
No. fish/100 m^2	3.0	4.4	2.2	4.8	3.4	3.6	4.6	6.2	130	14	9.5	5.6	1.5

These schools frequently occurred at the shallowest depths (<85 m) over rugged, rocky topography. Including transects where no schools were seen, the median and mean numbers, respectively, of small schooling rockfishes observed were 750 and 831 at depths <85 m, and 0 and 9.4 at depths >85 m. These schools, usually encountered about a meter off the bottom, often dove toward the bottom when alarmed by the submersible, with individuals dispersing into crevices, rubble, or among the stalks of large anemones.

23-31 August 1987. See Figure 3 for cluster analysis of habitat varied, we compared relative abundances among dives.)

	II: Deep mud and cobble							
Habitat:	IIA: Cobble		IIB: Mud					
Depth (m):	185-220	140-148	244	244	164-222	164-222	290-299	290-299
Species / Drive-transect:	3C	14	5A	5B	6B	6A	8A	8B
Rosethorn RF	27	21						
Yelloweye RF	1					1		
Lingcod			1					
Small RF		3	1		2			
Pigmey RF								
Ratfish			1			1	1	3
Sanddab								
Cottidae	16	17	5				3	
Greenstriped RF	1	21						
Zoarcidae	9	14	14	20	53	8	4	6
Canary RF		1						1
Yellowtail RF	2							
Kelp greenling								
Wolf-eel								
Large RF	5	4			2			
Longnose skate		2			1			1
Sharpchin RF	9		9		1	8	1	
Hagfish			1	1	1	14	7	5
Dover sole	11	29	8	3	10	4	6	12
Redbanded RF	1	1	4					
Darkblotched RF	1							
Splitnose RF		21	1	6				
Tiger RF								
Big skate			1					
Bathymasteridae								
Blenniidae								
Stripetail RF								
Agonidae	1	1	6	51	4	2	1	
Rajidae			1	1		1	1	3
Rex sole	4	2	8	9	4			2
Flatfish	10	3	8	13	2	5	1	1
Thornyhead	1		22				6	4
Arrowtooth Fl	1		1		4			
English sole		4				1	2	
Slender sole		2	2	13	16	65		1
Pacific hake			4					
Sablefish			4	1	2	1	65	67
Ragfish			1					
Sand sole			1					
No. fish types	16	16	22	10	13	12	12	12
No. fish/100 m^2	1.0	6.8	58	5.2	2.6	4.4	7.3	5.5

Solitary Benthic Rockfishes

We saw solitary benthic rockfishes on all dives. The rosethorn rockfish (10–15 cm in length) was the most ubiquitous of all fishes observed on our dives. They were seen on all dives between 67 and 305 m, except the two dives over mud bottom, and ranked first in abundance on 10 of 21 transects (Table 2). They usually occurred singly, resting on soft sediments near rocks, on flat rocks, and occasionally in the depressions of vase sponges. Shortspine thornyheads, *Sebasto-*

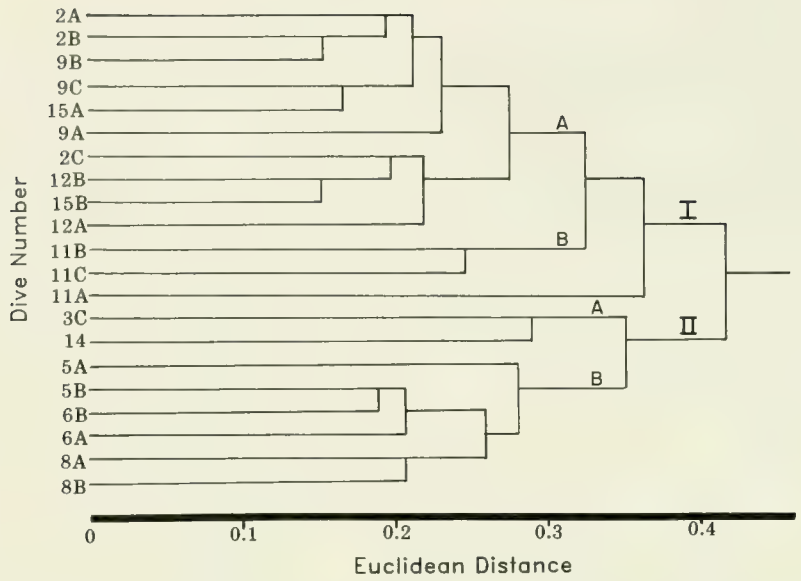

FIGURE 3.—Dendogram showing results of cluster analysis based on presence/absence of fish species from 21 transects. Dive numbers are shown along Y-axis and Euclidian distance along the X-axis. Roman numerals indicate the two major habitat groups and letters indicate subgroups (see Table 2).

lobus alascanus, and greenstriped rockfishes were usually in deep water on mud bottoms and in shallow water on mud or rocky bottoms, respectively (Tables 2, 3). Often thornyheads rested in shallow depressions in the bottom.

Largest concentrations of small- and intermediate-sized benthic rockfishes were seen during a dive at 149 m over rock (15A). Most of these were tentatively identified as sharpchin and pygmy, *S. wilsoni*, rockfishes. Their mean density on this transect was about 1.3/m^2 (Table 2). Pygmy; sharpchin; and Puget Sound, *S. emphaeus*, rockfishes were collected on this dive (Table 3). On another dive (not shown in Table 2), the densities of these small benthic rockfishes in areas of flat rocks, ledges, and cobble were as high as 5–10/m^2 at depths of 120–140 m. These fishes rested among rocks and ledges on the bottom but also swam one or two meters off the bottom. When frightened they often retreated into crevices and under rocks.

TABLE 3.—List of fishes (standard lengths in mm) collected with the slurp gun during five Mermaid dives onto Heceta Bank in August 1987.

Dive 3	
Slender sole	*Lyopsetta exilis* (186, 129)
Smootheye poacher	*Xeneretmus leiops* (170)
Dive 4	
Splitnose rockfish	*Sebastes diploproa* (181)
Bigeye starsnout poacher	*Bathyagonus pentacantha* (186)
Dive 6	
Rosethorn rockfish	*Sebastes helvomaculatus* (162)
Sharpchin rockfish	*Sebastes zacentrus* (132)
Dive 8	
Blacktail snailfish	*Careproctus melanurus* (227)
Dive 15	
Threadfin sculpin	*Icelinus filamentosus* (162)
Spotted cusk-eel	*Chilara taylori* (263)
Thornback sculpin	*Paricelinus hopliticus* (156)
Pygmy rockfish	*Sebastes wilsoni* (179, 148, 141, 136, 129, 117)
Sharpchin rockfish	*Sebastes zacentrus* (132, 92, 82)
Puget Sound rockfish	*Sebastes emphaeus* (101)

Large Schooling Rockfishes

Schools of large (30–50 cm) rockfishes were seen on five of the dives where bottom depths were less than 150 m. No schools of large rockfishes were seen in deeper water. These shallow-water schools were predominantly of yellowtail rockfish and occasionally of canary rockfishes. Other than an occasional canary or

[2]These fish had two white stripes, one above and one below the lateral line, with reddish pigmentation over the rest of the body.

yellowtail rockfish in a school of similar-sized yellowtail rockfish, all schools were comprised of fish of one species, all about the same size. Observers in the submersible sometimes located schools where echo-groups, probably caused by aggregations of large schooling rockfishes, were recorded by the surface vessel's echosounder. The sound scatterers were often prominent as spires close to topographic pinnacles or elevated rocky outcrops.

Yellowtail rockfish schools were attracted to and followed the submersible on several dives. On one dive, a school of 500–1000 fish stayed near the submersible for over an hour. The school either followed the submersible, or circled when it stopped, before abruptly turning away. Individual fish were usually 3–4 body lengths apart and could be clearly seen with ambient light at a depth of about 100 m. When the submersible lights were turned on, fish sometimes "flinched" but did not swim away. On another dive, a school of several hundred yellowtail rockfish were encountered while the submersible descended; they remained in view most of the way to the bottom. At first they actively swam downward, but at 100 m they passively sank, oriented head-down. When the thrusters were turned on, this school disappeared, but once the submersible was on the bottom, the school approached and swam around the submersible.

Large Near-Bottom Rockfishes

The best example of this category is the yelloweye rockfish. Large individuals of this species were seen in shallow water swimming above rock or cobble. Canary and yellowtail rockfishes, though more pelagic, sometimes were seen singly near the bottom. Although large rockfish usually were not resting on the bottom, yellowtail, splitnose (*S. diploproa* >30 cm), yelloweye, greenspotted (*S. chlorostictus*), and tiger (*S. nigrocinctus*) were observed doing so occasionally.

Rockfish Coloration. Splitnose rockfish sometimes changed color dramatically during and after collection. In situ, most individuals had strikingly red and white vertical bars extending almost to the ventral surface, but one that was chased blanched to almost all white. Another (181 mm SL) that was captured had lost its prominent white bars at the surface, appearing a dull red overall as shown in Eschmeyer et al. (1983). Straty (1987) also noted dramatic changes in the coloration of juvenile rockfishes in sita and after they were examined at the surface.

The yellowtail rockfish we observed had 3–5 very vivid large white spots above the lateral line. These spots faded to indistinct pale spots on live yellowtail brought to the surface by hook and line. The white spots on rosethorn rockfish were also less prominent on fish captured and brought to the surface than on those seen in situ.

Fishes Collected

In addition to several large benthic invertebrates, we collected 21 individuals and 12 species of fishes using the slurp gun (Table 3). Six species of rockfishes were also captured using hook and line from the support vessel: yellowtail, canary, yelloweye, rosethorn, greenspotted, and the bank (*S. rufus*) rockfishes. The last fish was not identified from the submersible. The liparidid *Careproctus melanurus* was also seen on several dives (but not during transects) and was collected by slurp gun.

DISCUSSION

The diverse physical habitats encountered during our dives correlated with differences in the species composition and abundances of fishes. Two species groups were identified: one primarily comprised of rockfishes in shallow water on rock and cobble, and one that included zoarcids, several species of flatfishes, agonids, and sablefish in deep water mostly over soft substrates. Greenstriped and splitnose rockfishes and shortspine thornyheads were most common over soft substrates, whereas most other scorpaenids were seen most frequently in rocky habitats in shallow water. Richards (1986) also noted that greenstriped rockfish were most abundant over fine-sediment habitats in the Strait of Georgia, British Columbia, whereas yelloweye rockfish preferred rock wall and more complex habitats at shallower depths.

Most species were broadly distributed (Table 2). There was much overlap in species distributions, and species associations were indistinct. Habitat type and depth varied together, however, with rock habitat occurring predominantly in shallow water and mud in deep water. Although cobble habitats were identified at two depths, these data were inadequate for examining bathymetric segregation of rockfish species within habitat types, as has been documented for

certain shallow-water species (Larson 1980; Hallacher and Roberts 1985).

Heceta Bank, and probably other rocky banks off the Pacific Northwest and Southeast Alaska, appear to be important juvenile nursery areas for rockfishes. Dense schools of pelagic juveniles and adult yellowtail rockfishes were observed only over the rocky, high-relief areas on the top of the bank, and high densities of benthic juveniles were found only on the flanks of the bank and not in deeper waters of the bank (Table 2). Straty (1987) and Carlson and Straty (1981) observed large schools of young rockfish near rocky pinnacles and boulder fields at depths <171 m off southeastern Alaska, and concluded that these areas were nursery grounds for rockfish. They collected specimens of Pacific ocean perch, *S. alutus*; sharpchin, pygmy, and Puget Sound rockfishes; and shortspine thornyheads on the bottom, species (with the exception of *S. alutus*) that we captured on Heceta Bank (Table 3).

Some of our submersible dives were close to locations previously sampled by trawl surveys of the Oregon Department of Fish and Wildlife (ODFW) (Barss et al. 1982). In the ODFW surveys, commercial trawls designed for catching rockfishes on rough terrain (Atlantic Western and Box Mystic trawls) were used with roller gear to keep the footrope off the bottom. The cod end of these nets was usually made of 11.4 cm mesh. During 1980–81, a total of 27 tows were made between 132 and 210 m, within about 4 km of Dive Site 11 (145 m) (Fig. 2).

Fish assemblages in trawl catches and in submersible observations from adjacent areas differed. Only 8 of the 25 trawl-caught species were seen from the submersible on Dive 11, and 7 of the species observed during the dive were not caught in trawls (Table 4). Five species of rockfishes, however, were among the most numerous 11 species by both methods. *Sebastes pinniger* dominated trawl catches by number and weight (comprising 88% of the total weight of the catches), but it was not seen many times from the submersible.

TABLE 4.—Composition of fishes by percentage calculated from numbers during submersible dives and caught in trawls from the same general area near Heceta Bank. The weight of individual species caught in trawl catches were converted to numbers of a species by dividing by the average weight of individuals.

Dive 11		Bottom trawl	
%	Species	%	Species
30.1	Schooling *Sebastes* spp.	76.2	*Sebaster pinniger*
29.4	*Sebastes helvomaculatus*	10.1	*Sebastes zacentrus*
10.7	*Sebastes* unidentified	2.5	*Sebastes flavidus*
7.2	*Sebastes zacentrus*	2.1	*Sebastes helvomaculatus*
4.6	*Sebastes pinniger*	1.5	*Merluccius productus*
4.2	*Sebastes ruberrimus*	1.2	*Ophiodon elongatus*
4.2	Zoarcidae	1.2	*Sebastes jordani*
1.5	*Sebastes crameri*	1.0	*Sebastes elongatus*
1.1	Rajidae	1.0	*Sebastes proriger*
1.1	*Sebastes diploproa*	0.6	*Sebastes brevispinnis*
1.1	*Raja rhina*	0.4	*Squalus acanthias*
0.8	*Hexagrammos decagrammus*	0.4	*Anoplopoma fimbria*
0.8	*Raja binoculata*	0.4	*Trachurus symmetricus*
0.4	*Sebastes elongatus*	0.3	*Hydrolagus colliei*
0.4	*Ophiodon elongatus*	0.2	*Sebastes ruberrimus*
0.4	Cottidae	0.2	*Sebastes paucispinis*
0.4	*Sebastes nigrocinctus*	0.2	*Microstopmus pacificus*
0.4	*Sebastes saxicola*	0.1	*Hippoglossus stenolepis*
0.4	*Eptatretus stouti*	0.1	*Parophrys vetulus*
0.4	Agonidae	0.1	*Glyptocephalus zachirus*
0.4	*Glyptocephalus zachirus*	0.1	*Sebastes entomelas*
		<0.1	*Oncorhynchus tshawytscha*
		<0.1	*Eopsetta jordani*
		<0.1	*Raja rhina*
		<0.1	*Atheresthes stomias*

Both of the assessment methods have biases, and differences between them are to be expected. The trawls were designed to avoid contact with the bottom and sampled a large volume of water at a greater distance above the seafloor and retained mostly large fishes, whereas the submersible was most effective for surveying small fishes on or close to the seafloor. Most large pelagic fishes probably avoided the submersible. Although yellowtail rockfish were attracted to the submersible, only a small fraction of the individuals in schools were visible from the viewing port. Differences in sampling locations and times undoubtedly contributed to differences in species composition. Thus quantitative surveys from submersibles appear to be most useful for assessing fishes closely associated with the sea floor, for comparing relative abundances among habitats, and for studying fine-scale distributions of fishes.

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Comparative Standing Stocks of Mesozooplankton and Macrozooplankton in the Southern Sector of the California Current System

The long-term (40-year) time series of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program has characterized low frequency changes in ocean circulation, macrozooplankton biomass, and ichthyoplankton and holozooplankton populations (Reid et al. 1958; Brinton 1981; Chelton et al. 1982; Smith 1985; McGowan 1985; Roesler and Chelton 1987). The Atlas series of the CalCOFI program provides extensive summaries of the hydrography of the California Current system and the large-scale distribution of its planktonic fauna (Atlas Nos. 1–30, Scripps Institution of Oceanography 1963–82). These investigations constitute an excellent foundation for studies ranging from experimental work with individual pelagic species to projections of global climate effects on ocean populations and production.

The primary emphasis of the zooplankton component of the CalCOFI program has been the larger macrozooplankton (>505 μm) and the ichthyoplankton. In the present study, we assess the biomass of the mesozooplankton (defined here as the zooplankton fraction passing through a 505 μm mesh net but retained in a 202 μm mesh net) in comparison with that of the historically sampled macrozooplankton. Efforts to close budgets of material and energy in the California Current system (Roemmich 1989) may require consideration of the contributions of the mesozooplankton to standing stocks and metabolic transformations. Further, given the selective nature of predation by planktivorous fish in this region (Arthur 1976; Koslow 1981), the mesozooplankton may be disproportionately significant as prey items to particular size classes of pelagic predators.

Materials and Methods

Comparisons of mesozooplankton and macrozooplankton standing stock were carried out between September 1986 and May 1987. A *ver*tically *r*etrieved *b*ongo (VERB) net frame was used to take paired zooplankton samples (Fig. 1). The net incorporated features of the Brown and Honegger (1978) vertical net and the McGowan and Brown (1966) oblique bongo net, with several differences. Unlike the Brown and Honegger net, the net rings did not hinge and presented less surface area. In contrast to the bongo net, the VERB frame did not pivot around a central axis, and the system was designed to filter only during vertical ascent rather than during oblique descent and ascent. The net mouth

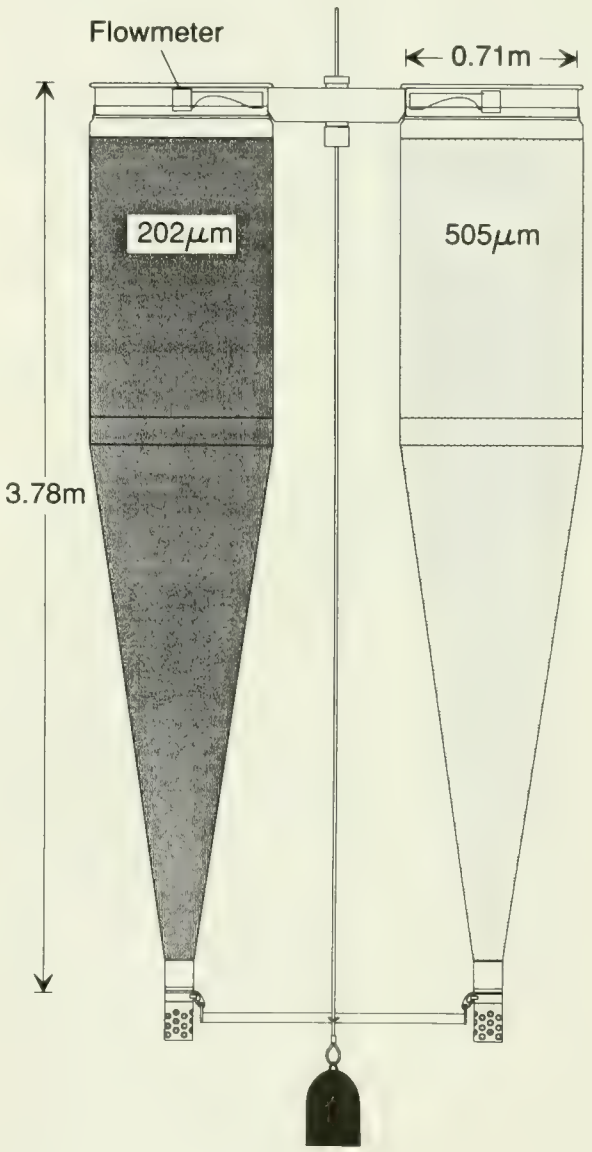

FIGURE 1.—Illustration of VERB frame and nets.

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openings were each 71 cm in diameter and the net open area ratio was no less than 5.0 (Tranter and Smith 1968). A 100 kg weight was secured to the end of the hydrowire. TSK flowmeters[1], modified to display flow counts digitally, were mounted inside both net rings. The frame was deployed with one 202 μm Nitex mesh and one 505 μm mesh net, each with rigid cod ends having apertures of the same mesh size.

The VERB frame was lowered at a speed of 40–50 m min^{-1} to 200 m and retrieved at 60 m min^{-1}. Each net filtered approximately 80 m^3 of water, minimizing clogging of the finer mesh net. Rapid deployment and recovery, combined with maneuvering the research vessel, served to minimize deviation of the hydrowire angle from the vertical. Wire angles were recorded at least four times during ascent.

Preliminary VERB net trials were carried out on cruise Verb1 (11–12 September 1986; see Figure 2). VERB deployments were then made on four CalCOFI cruises, designated 8609 (21–29 September 1986; N = 28 stations), 8611 (15–24 November 1986; N = 26), 8703 (5–14 March 1987; N = 27), and 8705 (3–12 May 1987; N = 30). The primary stations sampled were along two lines orthogonal to the coastline (lines 80 and 90); additional stations occupied the nearshore segment of lines 83 and 87 (Fig. 2). Time constraints precluded taking VERB samples at all CalCOFI stations.

Zooplankton samples were preserved in 10% formalin buffered with sodium borate. In the laboratory, the sample obtained with the 202 μm net was washed through a 505 μm mesh nested inside a 75 μm mesh, yielding a fraction between 202 μm and 505 μm ("mesozooplankton") and one greater than 505 μm ("macrozooplankton"). The sum of these two fractions is referred to as "total" net zooplankton, although it quite clearly omits the microzooplankton that are certain to be of considerable significance (Beers et al. 1980; Fenchel 1988). Biomass of zooplankton samples was determined first by measuring displacement volume (Ahlstrom and Thrailkill 1963), then by

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

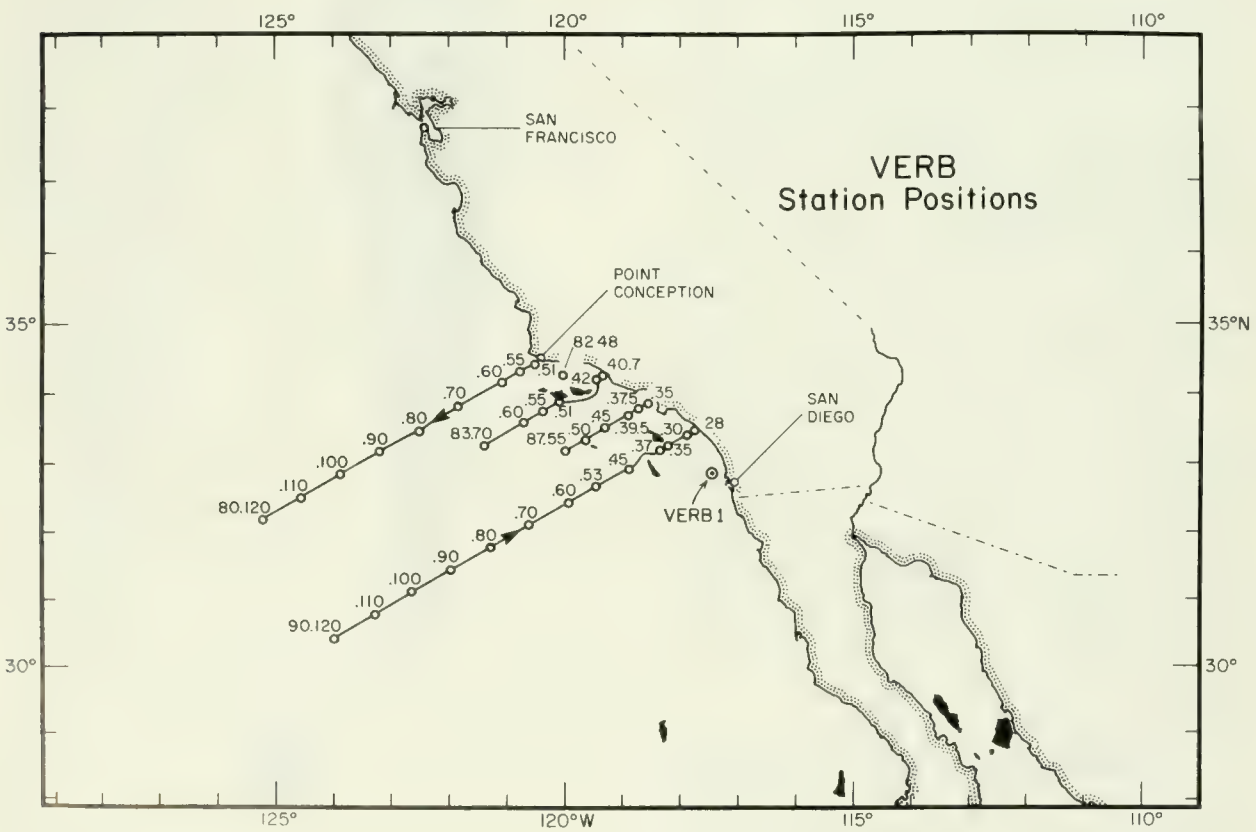

FIGURE 2.—Stations occupied in the southern sector of the California Current. Position of cruise VERB1 is noted, as well as the VERB zooplankton stations sampled on 4 CalCOFI cruises. Note that all indicated stations could not be sampled on every cruise.

measuring ash-free dry mass on a ¼ split of the sample obtained with a Folsom splitter. A split was filtered onto a pre-ashed Whatman GF/C filter, rinsed with a solution of 6% aqueous ammonium formate, and dried at 60°C. After weighing, the sample was ashed in a muffle furnace at 500°C for 4 hours then reweighed to determine ash-free dry mass by difference.

Standing stocks were expressed per unit volume, using the volume filtered by each net as determined from calibrated flow meters.

Water bottle samples for chlorophyll a (Chla) analyses were typically taken at 12–14 depths in the upper 200 m of the water column. Following filtration onto GF/C glass fiber filters, pigments were extracted in refrigerated 90% acetone in the dark and analyzed fluorometrically (Venrick and Hayward 1984). Chla between the surface and 150 m was integrated vertically using the trapezoidal rule. A complete report of chlorophyll data and detailed sampling information may be found in SIO References 87-7 and 87-19 (Scripps Institution of Oceanography 1987a, b).

RESULTS

Several characteristics of the VERB system were analyzed to determine its sampling bias, precision, and estimated filtration efficiency.

Right/Left Bias: A series of replicated vertical hauls was carried out with 202 μm nets mounted on both sides of the VERB frame. This was done over a 2½–3 h interval on 2 occasions. No bias was detected between the ash-free dry mass (AFDM) retained by the left and right nets on either 11 September ($N = 9$ hauls, $P > 0.10$, Wilcoxon Signed Rank test) or on 26 September ($N = 8$ hauls, $P > 0.10$).

Precision: Precision of replicated 202 μm vertical hauls, expressed as the coefficient of variation ($100 \times SD/\bar{x}$), was determined on 3 occasions, again over 2½–3 hours. Coefficients of variation of AFDM on 3 trials were 18.2% ($N =$ 18 samples, 9 hauls), 14.1% ($N = 16$ samples, 8 hauls), and 17.0% ($N = 13$ samples, 13 hauls).

Filtration Efficiency: Filtration efficiency of the 202 μm VERB net was compared against that of the 505 μm VERB net using the respective volumes of water filtered. Filtration efficiency of the 202 μm net averaged 99.4 ± 1.4% ($\bar{x}$ ± 95% C.L., $N = 126$ comparisons) of that of the 505 μm net, reflecting negligible clogging of the finer mesh net.

Wire Angles: The median wire angle (off the vertical) was 7°. Eighty-six percent of the angles were ≤12° ($N = 144$). Apart from unusually strong wind conditions when the net could not be deployed, wire angles could generally be maintained at acceptable levels (<10–12°) by maneuvering the vessel.

202 μm vs. 505 μm Nets: Retention characteristics of the 2 nets were compared from the >505 μm fraction displacement volume. The median ratio of the >505 μm displacement volume from the fine:coarse mesh nets was 1.17 (nonparametric 95% C.L.: 1.09–1.24, $N = 123$). The departure from a ratio of 1.00 probably reflects a difference between retention characteristics of the 505 μm plankton mesh in the field and in the laboratory. Larger organisms apparently show less escapement through 505 μm mesh under low pressure differential in the laboratory, compared with the high pressure differential across the mesh of a net under tow. To avoid introducing a systematic bias, further analyses are therefore restricted to the 2 fractions (<505 μm, >505 μm) collected by the 202 μm net.

Ash Content: The ash content of the 2 size fractions did not differ significantly ($P > 0.05$). Ash content as a percentage of total dry mass averaged 16.0% ± 0.9% ($\bar{x}$ ± 95% C.L., $N =$ 160) for the fraction <505 μm and 14.6% ± 0.7% for the fraction >505 μm.

Standing Stocks: The relation between displacement volume and AFDM appeared relatively linear when expressed on a log-log scale (Fig. 3A). However, closer inspection revealed that the slope of this relation differed for the 2 size fractions ($P<0.001$, Analysis of Covariance). Hence a joint regression line was inappropriate. When replotted separately on linear axes, the difference in these relations was more apparent (Fig. 3B, C). A rectilinear function provided an adequate least squares fit for the fraction <505 μm (Table 1). However, the relation was nonlinear for the fraction >505 μm. Use of a curvilinear function (Table 1) decreased the residual sum of squares and removed the serial correlation of residuals that was apparent in a straight line fit ($P < 0.05$). For the fraction >505 μm, a linear relation was a particularly poor

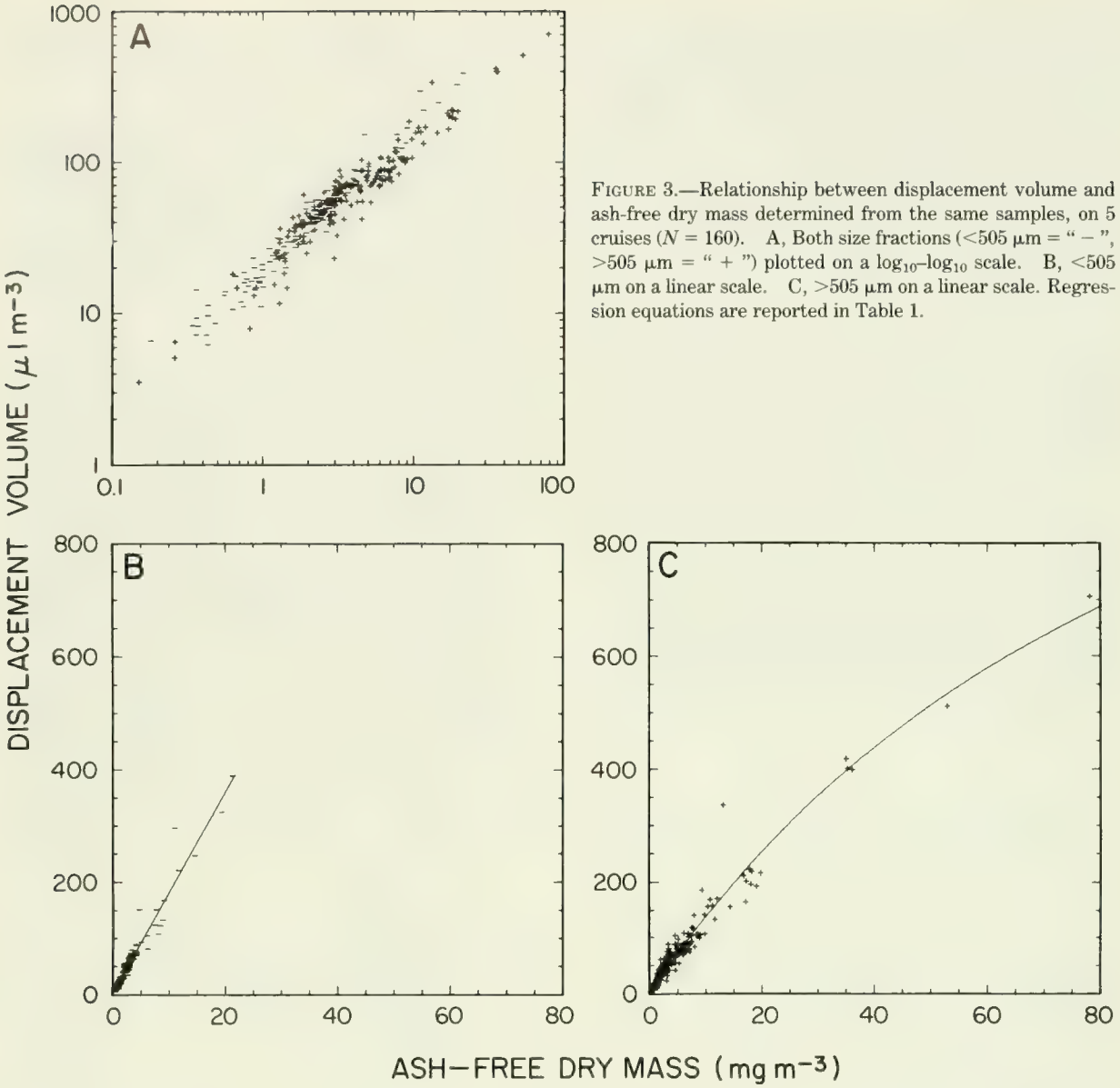

FIGURE 3.—Relationship between displacement volume and ash-free dry mass determined from the same samples, on 5 cruises (N = 160). A, Both size fractions (<505 μm = " – ", >505 μm = " + ") plotted on a $\log_{10}$–$\log_{10}$ scale. B, <505 μm on a linear scale. C, >505 μm on a linear scale. Regression equations are reported in Table 1.

descriptor at low AFDM values. The F-statistic was inappropriate for testing the goodness-of-fit of a nonlinear curve (Draper and Smith 1981), but the F-ratio reported in Table 1 provided a relative indicator of the adequacy of the regression equation. The fitted curve in Figure 3C was merely an empirical fit that was not meant to imply any theoretical relation. Because of this nonlinearity, perhaps caused by the compressibility of larger organisms at high biomass levels, AFDM was used for subsequent comparisons.

Since both displacement volume and AFDM have natural variability, a functional regression (Laws and Archie 1981) would be a more appropriate statistical model to apply to the data in Figure 3. However, the need for a nonlinear relationship for the >505 μm fraction complicates the use of a functional regression model. For consistency, the fit for both size fractions is therefore based on predictive regressions with the attendant possibility of introducing biased estimators (Sokal and Rohlf 1981). Users of functional regressions should note that the equation for estimating the confidence interval of the regression slope reported in Jensen (1986; equation 14) is in error.

A comparison of mesozooplankton and macrozooplankton standing stocks for four pooled CalCOFI cruises is illustrated in Figure 4. The median contribution of the mesozooplankton to

TABLE 1—Regression relationships between displacement volume (DV; $\mu L\ m^{-3}$) and ash-free dry mass (AFDM; $mg\ m^{-3}$). *F*-ratio designates the ratio of regression mean square: residuals mean square. Regression *P*-value indicates the significance of a linear regression, and the residuals *P*-value indicates the significance of the first order serial correlation of regression residuals. $N = 160$ for both size fractions.

Size fraction	Equation	*F*-ratio	Regression *P*-value	r^2	Residuals *P*-value
<505 μm	DV = 17.86(AFDM) + 3.86	2,869.1	<0.001	0.938	>0.10
>505 μm	$DV = \frac{1594.7(AFDM)}{105.5 + AFDM}$	2,725.6	—	—	>0.10

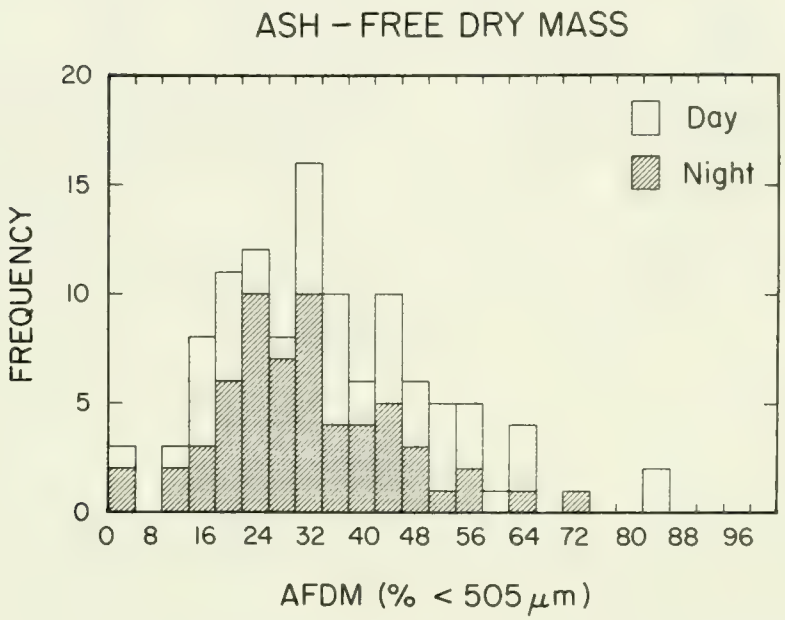

FIGURE 4.—Frequency distribution of the percentage of ash-free dry mass in the fraction <505 μm, from 4 CalCOFI cruises ($N = 111$).

the total standing stock was 30.2%. Partitioned by time of sampling, the day mesozooplankton averaged 35.0% and the night mesozooplankton 28.1% of total standing stock. Day and night medians differed significantly ($P < 0.05$, Mann-Whitney U test). The higher proportion of macrozooplankton (>505 μm) in nighttime samples probably reflects nocturnal vertical migration of larger zooplankton into the upper 200 m of the water column or, perhaps, diurnal net avoidance. At individual stations, the mesozooplankton contribution ranged up to 82% of the total.

Despite considerable variance in the relationship, zooplankton standing stocks were positively correlated with the Chla concentration (Fig. 5). This relation, apparently curvilinear, is illustrated as log AFDM plotted against the log maximum Chla concentration in vertical profile at each station for the fraction <505 μm (Fig. 5A: $r = 0.73$, $P < 0.001$, Spearman's rank correlation, $N = 110$) and that >505 μm (Fig. 5B: $r = 0.70$, $P < 0.001$, $N = 110$). When plotted against the log chlorophyll integrated to 150 m the correlation coefficients were slightly smaller (<505 μm: $r = 0.71$; >505 μm: $r = 0.64$).

The relative contribution of mesozooplankton to total standing stocks varied independently of Chla concentration. Neither in the day samples ($r_s = -0.117$, $P > 0.10$, $N = 49$) nor in the night samples ($r_s = 0.060$, $P > 0.10$, $N = 61$) was the fraction of standing stock <505 μm associated with Chla (Fig. 6).

Sufficient samples to analyze cross-shore gradients in total standing stock and in the percentage of standing stock contributed by the mesozooplankton were obtained only along lines

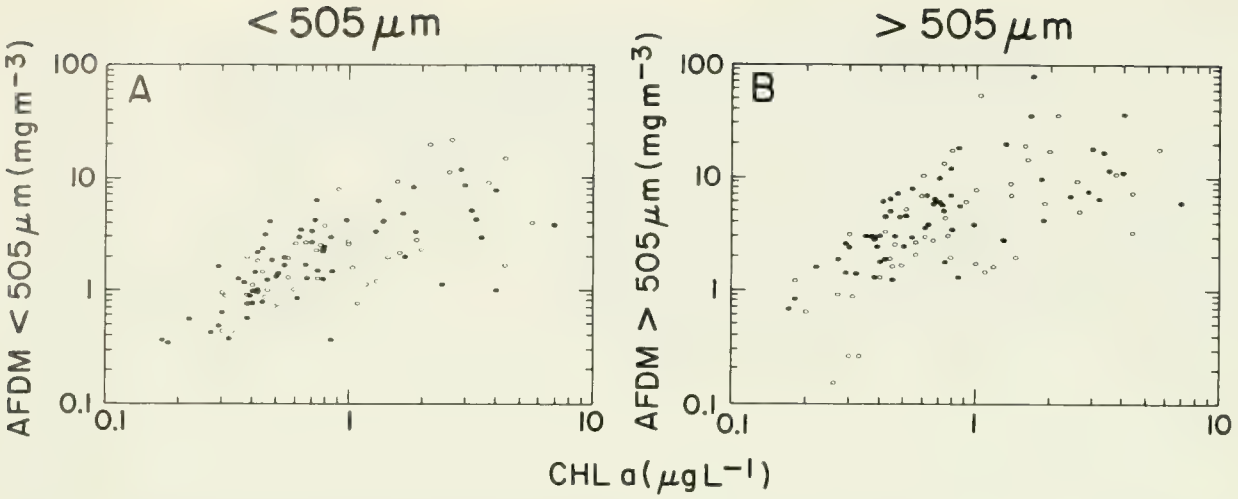

FIGURE 5.—Relationship between ash-free dry mass (AFDM) and maximum Chl*a* concentration, from 4 CalCOFI cruises. Open circles are day samples, closed circles are night samples. A, AFDM <505 μm; B, AFDM >505 μm.

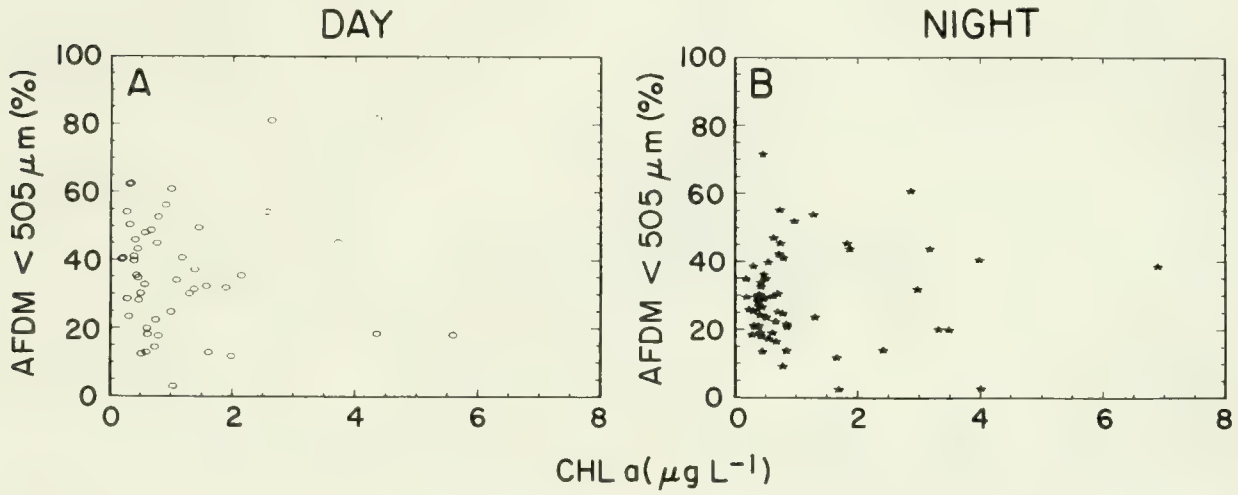

FIGURE 6.—Relationship between the percentage of ash-free dry mass in the fraction <505 μm and Chl*a* concentration, from 4 CalCOFI cruises. A, Day samples; B, night samples.

80 and 90. (Even so, the two offshore stations along line 80 were sampled only on cruise 8609.) Samples from lines 83 and 87 are included in Figures 3–6 but were not analyzed for spatial trends. Along both line 80 and line 90 the 4-cruise average of total AFDM decreased in the cross-shore direction (Fig. 7A, B). On individual cruises a secondary maximum of standing stock often occurred offshore along line 80 (e.g., cruises 8609, 8705) and line 90 (e.g., cruises 8609, 8703, 8705).

The percentage of zooplankton standing stock <505 μm also exhibited some cross-shore trends. On both lines 80 and 90, the median value was highest at the station closest to shore (Fig. 7C, D). On line 80 the median value first decreased then remained relatively constant in the offshore direction. On line 90 the median value decreased to station 80 then appeared to increase again at the more offshore stations. (This apparent offshore increase at stations 110 and 120 may have been influenced by a higher incidence of daytime samples.) That is, mesozooplankton appeared to make a larger contribution to standing stock at the most inshore stations and possibly at the most offshore stations along line 90.

DISCUSSION

These results demonstrate that, on average, approximately one third of the >202 μm zoo-

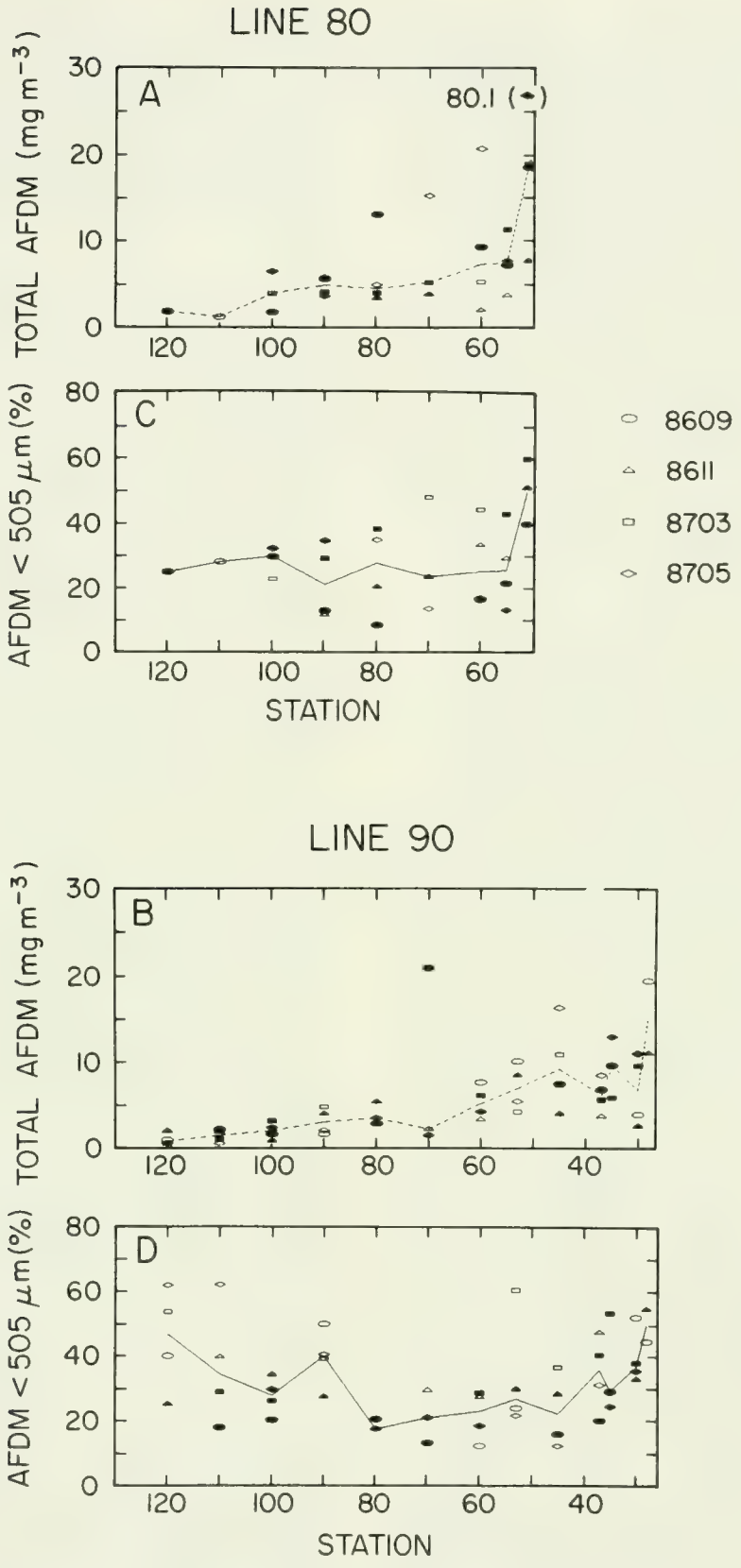

FIGURE 7.—Cross-shore distributions of total ash-free dry mass along (A) line 80 and (B) line 90, and percentage of ash-free dry mass in the fraction <505 μm along (C) line 80 and (D) line 90. Stations along lines 80 and 90 are aligned vertically. Dashed and solid lines illustrate the median values.

plankton standing stock is in the mesozooplankton fraction in this sector of the California Current system. Considerably higher contributions occur in some regions and on some occasions. It is difficult to estimate the contribution of this standing stock to heterotrophic processes such as grazing, oxidative metabolism, and fecal pellet fluxes without further information on the species composition of the two size fractions. However, because physiological processes depend on body mass (Banse and Mosher 1980), the mesozooplankton would contribute disproportionately to these water column processes.

Consider, for example, *Paracalanus parvus*, a relatively small-bodied copepod representative of the mesozooplankton retained by a 202 μm mesh net, and the larger copepod *Calanus pacificus* and euphausiid *Euphausia pacifica*, the latter two representative of the macrozooplankton captured by a 505 μm mesh net. The maximum daily specific ingestion rate of *P. parvus* females is 1.0–2.2 d^{-1} (varying on a carbon and a nitrogen specific basis, Checkley 1980), while that of *Calanus pacificus* is ca. 0.4 d^{-1} (Frost 1972) and that of adult *Euphausia pacifica* is ca. 0.08 d^{-1} (Ohman 1984). Based on these mass-specific rates, if 30.2% of the zooplankton standing stock were *P. parvus*-like organisms and the remainder were evenly split between *Calanus*-like and *Euphausia*-like organisms, the mesozooplankton could account for 79% of the grazing pressure. The presence of larvaceans and salps would alter this estimate because these gelatinous organisms are relatively large but have higher specific rates of metabolism than most crustacean zooplankton (Alldredge and Madin 1982). Furthermore, the estimate ignores the presence of omnivores and predators and assumes, unrealistically, food-satiated ingestion rates for all taxa. Nevertheless, the mesozooplankton is doubtless a significant contributor to heterotrophic processes.

The increased contribution of the mesozooplankton in the most inshore domain may reflect the presence of early developmental stages of zooplankton species that show relatively high rates of reproduction inshore (Brinton 1976; Checkley 1980; Smith et al. 1986). The possible trend toward a larger contribution of mesozooplankton offshore along line 90 requires corroboration. Much further to the west, in the oligotrophic central North Pacific, 20–40% of the zooplankton standing stock collected with a 183 μm net was <500 μm (Rodriguez and Mullin 1986).

The relation between displacement volume and ash-free dry mass for both size fractions combined is qualitatively similar to that reported in Wiebe et al. (1975, fig. 4a); however, their regression includes several size categories and their dry mass values apparently included ash, so that the two studies are not strictly comparable.

Whether the relative importance of mesozooplankton varies through time, such as during El Niño-Southern Oscillation (ENSO) conditions, is unknown. Smith (1985) documented an appreciable compositional change within the macrozooplankton during the strong ENSO of 1957–59. For example, comparing 1956 and 1958, the average thaliacean (primarily salp, larvacean, doliolid) biomass decreased 27-fold while the total copepod biomass decreased by only ½ during this ENSO (Smith 1985), suggesting differential responses to ENSO events by different members of the pelagic food web.

How such compositional changes within the macrozooplankton might relate to changes in the relative importance of mesozooplankton organisms is not obvious. Since phytoplankton concentrations can decrease markedly during ENSO conditions (Fiedler 1984), the argument could be made that smaller zooplankton, which generally have lower food requirements to sustain growth and reproduction (Huntley and Boyd 1984), might increase in relative abundance. However, the lack of correlation between the fraction of zooplankton <505 μm and Chla suggests that chlorophyll alone is too simple a measure of food availability. Microzooplankton may also be an important prey source. And it should be noted that a model based on energetic considerations makes a contradictory prediction, namely increased body size in oligotrophic regions (Gerritsen and Kou 1985). Additional information beyond food requirements must also be considered, including life history traits and species composition of the constituent zooplankton, as well as mesoscale circulation effects on species distributions (Haury et al. 1986).

The present evidence for the significance of the mesozooplankton in the California Current system is based upon a bulk measure of zooplankton standing stock. Future efforts directed toward understanding the mechanisms of response of planktonic organisms to environmental change should take account of species-specific responses of the mesozooplankton.

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Tuna Larvae Abundance: Comparative Estimates from Concurrent Japanese and Australian Sampling Programs

When estimating the absolute abundance of organisms, the accuracy and bias of sampling methods should be assessed (Andrew and Mapstone 1987). In ichthyoplankton sampling the absolute abundance of organisms will probably never be known; the characteristics of accuracy and bias in different sampling methods can only be inferred by concomitant sampling of the same population. The Fishery Agency of Japan Far Seas Fisheries Research Laboratory (FSFRL) has used a 2 m ring net to sample ichthyoplankton for many years. It has been the principal tool for sampling tuna larvae, particularly southern bluefin tuna, in the eastern Indian Ocean (Yabe et al. 1966; Ueyanagi 1969; Yonemori and Morita 1978; Yukinawa and Miyabe 1984; Yukinawa and Koido 1985). The net routinely samples large volumes of water (approximately 5,000 m^3 in a 30-min oblique tow), yet catches of tuna larvae on these surveys are generally low. These low catches may reflect a naturally low abundance of tuna larvae, a contention supported by previous studies (Wade 1951; Strasburg 1960; Klawe 1963; Richards 1969; Richards and Simmons 1971; Conand and Richards 1982). In this paper we compare catches of tuna larvae by traditional Japanese methods with those developed by CSIRO Division of Fisheries for quantitative surveys. A series of simultaneous tows were made by the CSIRO, FRV *Soela* and the FSFRL, FRV *Shoyo Maru* on the southern bluefin tuna spawning grounds in the east Indian Ocean in January 1987.

Methods

Two identical 2 m ring nets were deployed concurrently by the FSFRL (Fig. 1, Table 1) in surface and oblique tows. For the oblique tow, a predetermined length of warp (approximately 130 m) was rapidly paid out from the stern so that the net reached a depth of 30 m (approximately 4–10 minutes). The warp was then retrieved at a fixed rate until the net reached the surface (approximately 21–26 minutes). The tow profile actually achieved was determined after the tow from traces made by the depth distance recorder. The 20-min surface tow was deployed close to the hull on the starboard side, amidships, with approximately 7/8 of the net below the surface, fishing a depth range of 0–1.75 m.

Two identical 70 cm ring nets were deployed concurrently by CSIRO (Fig. 1, Table 1) in surface and oblique tows. The oblique tow fished from the surface to the thermocline (the thermocline during the experiment was at approximately 32 m) to cover the full known depth range of the tuna larvae (CSIRO, unpubl. data). An operator, guided by real-time depth information from a sensor on the net, produced a V-shaped tow profile, with a descent time of approximately 8 minutes and an ascent of 12 minutes. The surface tow was deployed for 10 minutes, concurrent with the oblique tow, from a boom on the port side amidships, clear of the wake of the vessel. It was towed approximately 0.5 m under the surface, oscillating between about 0 and 2 m due to the roll of the vessel in the 0.5 m swell.

The volume of water filtered for each net was calculated in the following ways. The volumes filtered by both surface and oblique tows with the 70 cm net were calculated from the distance travelled, measured by calibrated flowmeter readings inside the net, and the mouth area of the net. Volumes filtered by oblique tows with the 2 m net were calculated from the distance travelled (determined from the depth distance recorder behind the net) and the mouth area of

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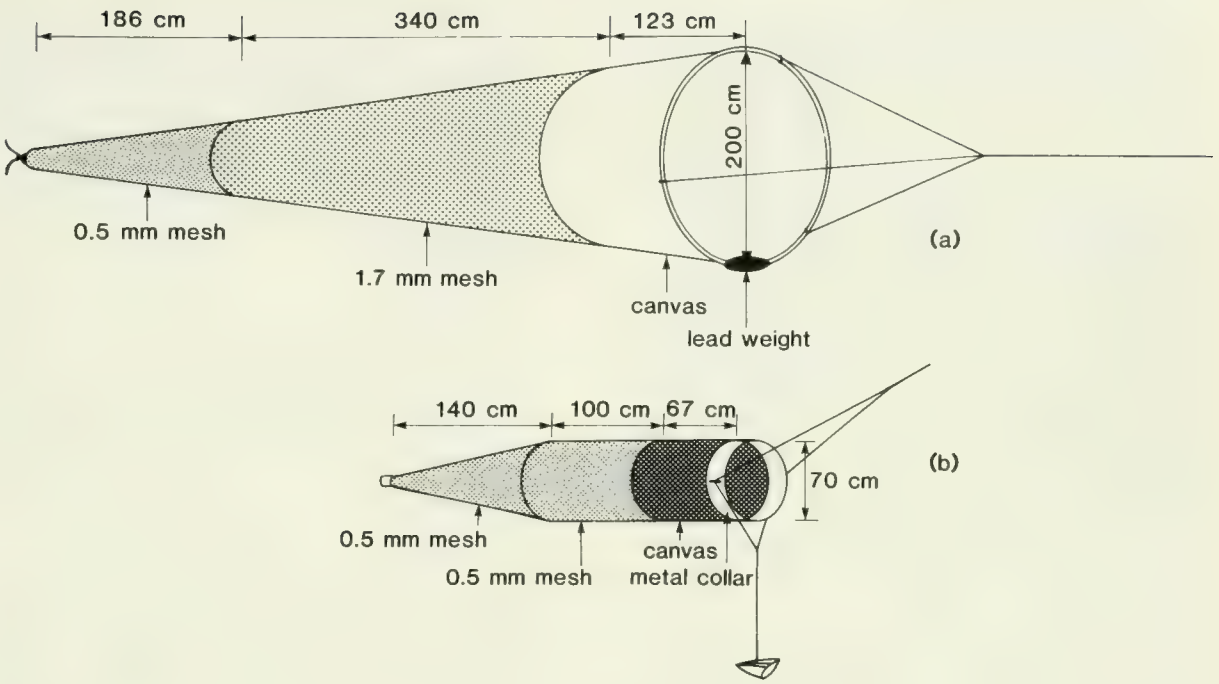

FIGURE 1.—The 2 m and 70 cm nets in their deployed configuration.

TABLE 1.—Specifications of the 70 cm net used by CSIRO and the 2 m net used by FSFRL.

Specification	70 cm net	2 m net
Shape	cylindrical-conical	conical
Mouth opening	70 cm internal diameter, circular, maintained by aluminium collar 18 cm wide	200 cm internal diameter, circular, maintained by galvanized iron pipe
Mouth area	0.385 m^2	3.142 m^2
Net material	Estal monofilament, plain with mesh aperture of 0.5 mm throughout	forward section of multifilament, twist lock with mesh aperture of 1.7 mm, followed by nylon monofilament, plain with mesh aperture of 0.5 mm
Net colour	dyed dark blue	natural (white)
Canvas collar	67 cm width	123 cm width
Bridle	two-wire	three-rope
Depressor	22 kg Scripps attached by two-wire bridle	30 kg weight attached to frame
Flowmeter	General Oceanics[1] mechanical, attached inside mouth frame 17 cm from rim	Tsurumi-Seiki depth distance recorder, towed behind the net
Cod end	solid, thread mounted PVC with 0.5 mm stainless steel drainage screen	netting tied at end to form soft cod end

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA

the net. The 2 m net used at the surface was not fitted with a meter so the distance travelled was estimated from the ships speed (2 knots) and the tow duration (20 minutes). Only the submerged mouth area of the 2 m net was used to calculate the volume filtered.

The *Soela* and the *Shoyo Maru* met on 27 January 1987 at lat. 15°S, long. 116°E. The two

vessels, approximately 250 m apart, steamed at 2 knots. Concurrent surface and oblique tows were made by both vessels at six stations in daylight between 1300 and 1700 h local time; the start of tows on each vessel was co-ordinated by radio and visual communication. The distance separating the two vessels during the tows was determined by radar.

The plankton samples taken by the 70 cm net were preserved in 95% ethanol and those from the 2 m net in 10% formalin. Samples were sorted, and tuna larvae identified to species (where possible) and measured (standard length) in the respective laboratories. At FSFRL the samples were sorted in petri dishes with the unaided eye, whereas at CSIRO samples were sorted in a rotatable sorting ring under a dissecting microscope with dark-field illumination. Both laboratories used a dissecting microscope to aid in identification of larvae.

The relative efficiency of the 70 cm and 2 m nets was described by ratios of the mean catch per unit volume for each method of deployment (surface and oblique tows) assuming that small catches are more prone to error than large catches (Snedecor and Cochran 1967). The significance of differences in the number of tuna larvae per unit volume collected by the 2 m and 70 cm net in surface and oblique tows was tested by two-factor ANOVA of split-plot design (Winer 1971). The data were log $(x + 1)$ transformed to make variances homogeneous (Cochran's test; $C = 0.47$; df = 4,5; $P > 0.05$). Differences in the mean lengths of larvae caught by net type and tow type were analyzed by the Kruskal-Wallis test (corrected for ties), and multiple comparisons (with unequal sample sizes) were made using the Dunn test (Zar 1984).

Results

The stations were at approximately 2.4 km intervals and the vessels were, on average, 260 m apart during tows. The range of volumes filtered by net and tow type was 505-560 m^3 for a 70 cm net in oblique tow; 244-307 m^3 for a 70 cm net in surface tow; 4,600-5,650 m^3 for a 2 m net in oblique tow; and 3,600 m^3 for a 2 m net in surface tow. Mean displacement volume of plankton caught by the 70 cm net was higher in oblique tows (27.3 mL/1,000 m^3) than in surface tows (4.4 mL/1,000 m^3). Both surface and oblique tows with the 70 cm nets caught a total of 283 tuna larvae whereas the 2 m nets caught 123 (Table 2). The species composition of the sorted and identified catches was similar except for an unidentified component in the CSIRO catches. This was due to a more conservative approach to identification by the less experienced CSIRO staff. The species composition of the FSFRL samples suggests that most CSIRO *Thunnus* spp. were probably *Thunnus alalunga*.

TABLE 2.—Numbers of tuna larvae taken in 2 m net hauls (surface and oblique) by FRV *Shoyo Maru* and in 70 cm net hauls (surface and oblique) by FRV *Soela*.

Species	2 m net		70 cm net	
	n	%	*n*	%
Thunnus maccoyii	9	(7.3)	21	(7.4)
Thunnus obesus	3	(2.4)	0	(0)
Thunnus albacares	7	(5.7)	0	(0)
Thunnus alalunga	77	(62.6)	78	(27.6)
Thunnus albacares/alalunga	25	(20.0)	66	(23.3)
Katsuwonus pelamis	1	(0.8)	1	(0.4)
Thunnus spp.[1]	0	(0)	117	(41.3)
Total	123		283	

[1]Small larvae 2.1–3.8 mm SL but usually < 3.3 mm SL not having the pigment pattern needed to distinguish to species.

The mean catch in the 70 cm net in oblique and surface tows was 16.5 and 144.7 tuna larvae/1,000 m^3, respectively. Catches in the 2 m net in oblique and surface tows were much lower, 1.4 and 3.7 tuna larvae/1,000 m^3, respectively. The ratio of the mean catches (70 cm net/2 m net) was 11.8 (SE ± 3.5) for oblique tows and 39.6 (SE ± 10.7) for surface tows. Catches in the 70 cm net were significantly higher than in the 2 m net ($F = 140.9$; df = 1,5; $P < 0.001$) and catches in surface tows were significantly higher than oblique tows ($F = 11.3$; df = 1,10; $P < 0.01$). The difference in catch between surface and oblique tows was mainly attributable to the 70 cm net; hence, there was a significant interaction between net type and tow depth ($F = 6.1$; df = 1,10; $P < 0.05$) (Fig. 2).

There were significant differences in the mean lengths of larvae caught by net and tow type (Kruskal-Wallis test; $H = 21.74$; df = 3; $P < 0.001$). The mean length of tuna larvae caught in the 2 m oblique tows (4.03 mm) was significantly greater (Dunn test; $P < 0.05$) than those caught in 2 m surface tows (3.60 mm), 70 cm oblique tows (3.56 mm), and 70 cm surface tows (3.65 mm) (Fig. 3). This was due to a lower proportion of small larvae (and the absence of larvae less

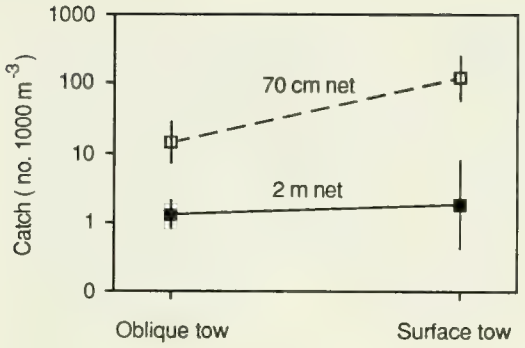

FIGURE 2.—Geometric mean catch (1,000 m^{-3}) by the 70 cm and 2 m net in surface and oblique tows and 95% confidence intervals. Catch has been plotted on a log scale.

than 3.0 mm) rather than an increased proportion of large larvae in the 2 m oblique tow (Fig. 3).

Discussion

No attempt was made to control the many variables that could contribute to the difference in abundance estimates of the two sampling programs; we were more interested in the relative effectiveness of existing methods rather than in the effects of specific variables. CSIRO estimates based on surface and oblique tows were 93 and 13 times greater than corresponding estimates by FSFRL. The most obvious and

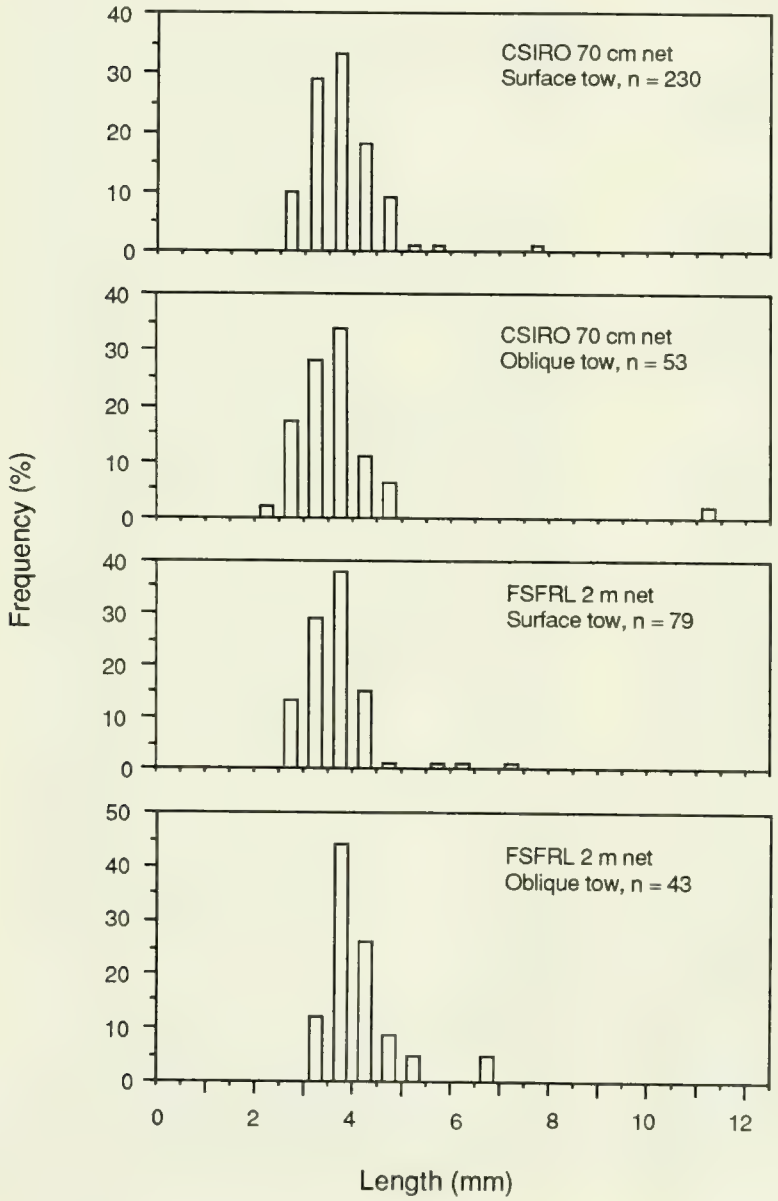

FIGURE 3.—Length-frequency distribution of tuna larvae caught in 2 m net hauls (surface and oblique) by FRV *Shoyo Maru* and in 70 cm net hauls (surface and oblique) by FRV *Soela*.

arguably the most important difference between the nets used by the programs is that the FSFRL 2 m net has 1.7 mm mesh in the forward section. Larvae are apparently lost by mesh escapement through this section. This type of multimesh construction may "herd" the larvae, but this advantage seems to be greatly outweighed by escapement. If we assume that the 1.7 mm mesh retains no larvae, then catches by the 2 m net can be recalculated for the 1.05 m diameter opening of the remaining 0.5 mm mesh section. This gave mean catches of 12.3 and 5.09 larvae/1,000 m^3 for surface and oblique tows, respectively. Based on this assumption, the CSIRO catches were still 12 times larger than FSFRL catches for surface tows and about 3 times greater for oblique tows. Reanalysis of the ANOVA using these data produced the same differences and levels of significance as in the original analysis. This demonstrates that, although escapement through the 1.7 mm mesh may account for a significant loss of larvae, other factors must also contribute to the lower catches by the FSFRL program.

A number of factors could cause increased avoidance of the 2 m net and hence reduce catches. While it might be expected that the 2 m net would reduce net avoidance by virtue of its size, this may have the opposite effect owing to an increase in the reaction distance to it (Barkley 1964, 1972; Wiebe et al. 1982). It has been well established that samplers that have no bridle obstructing the mouth (such as bongo nets and the 70 cm net) are far more efficient samplers than nets with conventional triple-rigged bridles (such as the 2 m net) owing to increased avoidance of the latter (Posgay and Marak 1980). Other factors that could increase avoidance of the 2 m net include the 30 kg depressor attached directly to the frame of the net, increasing visibility and turbulence and hence the reaction distance, and the high visibility of the undyed (white) net compared with the blue 70 cm net (Smith and Richardson 1977).

The volume filtered by the 2 m net may also have been overestimated as it was measured outside the net by the depth/distance recorder. This would result in lower apparent catch rates. Reduced filtering efficiency due to clogging in the 0.5 mm section, which may be a problem with the 2 m net because of its low open area ratio (Tranter and Heron 1967), would not be detected. In the laboratory, the sorting of larvae from samples without the aid of a microscope could result in extraction of fewer larvae in the FSFRL program, thus further reducing apparent catches.

The 70 cm net caught greater numbers of tuna larvae in the surface tow relative to the oblique tow than did the 2 m net. Catches in the 2 m net surface tow may have been reduced by increased avoidance because the net is towed very close to the hull of the *Shoyo Maru*. Alternatively, the oblique tow may have oversampled surface waters where the larvae are more abundant. The tow profiles for the 2 m oblique tow do suggest that this occurred to some extent. Clogging of the 0.5 mm mesh in the surface tows would not account for the disproportionately low catches because clogging would have been more likely to occur in the oblique tows which caught greater volumes of plankton.

We are not sure of the reasons for the differences in lengths of larvae caught by the two programs because of the many possible confounding factors. The greater mean length of larvae in the FSFRL oblique tows was due to fewer small larvae rather than to greater catches of large larvae. This could have resulted from differences in net deployment or in processing of samples, or could simply have been an artifact of the small sample size collected by the 2 m net in oblique tows. It would not have been due to differential loss of small larvae through the 1.7 mm mesh because this did not occur in surface tows with the same net.

The estimated abundance of tuna larvae in CSIRO surface and oblique tows was much higher than the corresponding estimates by the FSFRL program. We assume that larger catches are more accurate than smaller catches because towed nets are inefficient samplers owing to avoidance and mesh escapement (Clutter and Anraku 1968; Murphy and Clutter 1972; Clarke 1983) and subsequent treatment of samples (removal from nets, sorting, and enumeration) is likely to lead to the loss of larvae resulting in underestimation rather than overestimation. This would suggest that the 70 cm net as it is deployed in the CSIRO program is more efficient at catching tuna larvae than the 2 m net used in the FSFRL program, despite its much smaller size.

Acknowledgments

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CSIRO and FSFRL samples were carried out at the respective laboratories, and we are grateful for the assistance of J. Young, J. May, O. Augustine, and P. Bonham. We thank B. Hansen for drawing the figures, S. E. Wayte for statistical advice, and J. M. Leis, R. E. Thresher, V. Mawson, and F. R. Harden Jones for reviewing the manuscript and suggesting many improvements.

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Longbill Spearfish, *Tetrapturus pfluegeri*, Incidentally Caught by Recreational Billfishermen in the Western North Atlantic Ocean, 1974–86

Recreational billfish surveys have been conducted annually by the National Marine Fisheries Service (NMFS), Southeast Fisheries Center (SEFC), in the Atlantic Ocean off the U.S. east coast, the Gulf of Mexico, the Bahamas, and the Caribbean Sea since 1971. During these surveys, biological samples were collected to determine age and growth parameters, and reproductive biology; and to monitor catch and effort trends of all billfish species. These species include the sailfish, *Istiophorus platypterus*, white marlin, *Tetrapturus albidus*, blue marlin, *Makaira nigricans*, and longbill spearfish, *Tetrapturus pfluegeri*. With the exception of the longbill spearfish, these species have received considerable attention from fisheries scientists (Nakamura 1985). Owing to the rarity of longbill spearfish in coastal waters, there have been very little fisheries information and biological data published (Robins 1975; Nakamura 1985). All spearfish data collected by the NMFS/SEFC during the annual recreational billfish surveys are summarized in this note.

The longbill spearfish is an epipelagic species found in offshore waters throughout the Atlantic Ocean extending from lat. 40°N to 35°S (Nakamura 1985). These fish are commonly caught by foreign longline vessels fishing offshore for tuna (Ueyanagi et al. 1970) but are rarely caught by recreational vessels fishing closer inshore for sailfish and marlin (Beardsley and Conser 1981). Longbill spearfish are incidentally caught by recreational fishermen while trolling for the more popular sailfish and marlin.

Spearfish are caught during the months of March through September, but particularly during the summer (Fig. 1). The shortened seasons for catches in the temperate Gulf of Mexico and Atlantic, contrasted with the extended season in the tropical Caribbean, indicate that spearfish prefer warm offshore water. The fish were caught during daylight, with the majority being caught between the hours of 0800 and 1400 (Table 1). Spearfish feed on a variety of epipelagic organisms (Ovchinnikov 1979). Limited data (29 specimens) showed no distinct preference for either artificial or natural (dead) trolled baits (Table 1).

The average length and weight of the spearfish was 151.8 cm (lower jaw fork length, SD 24.3, $N = 35$) and 14.7 kg (SD 6.3, $N = 38$). These lengths and weights are similar to the

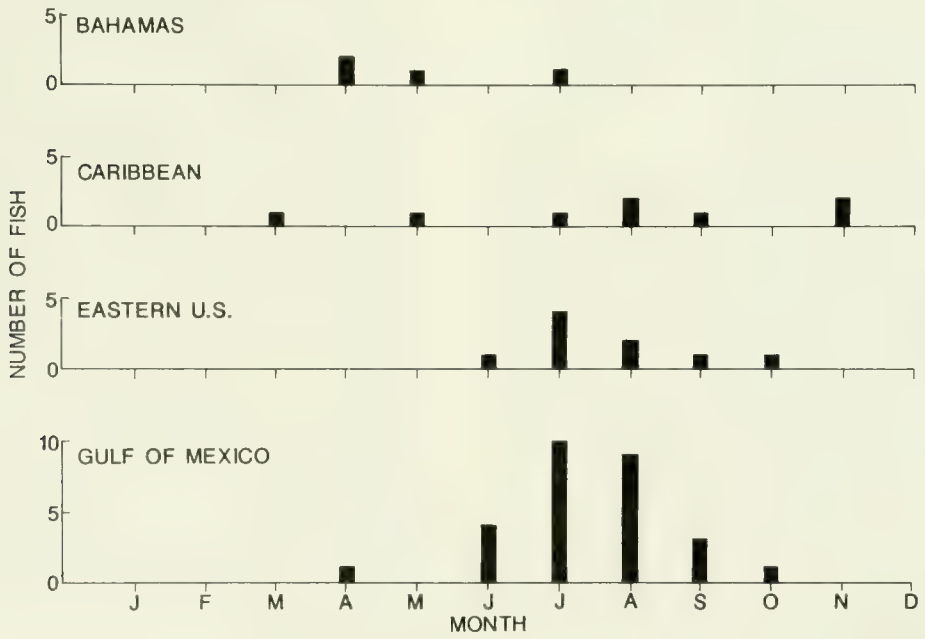

FIGURE 1.—Seasonality, by geographic area, of spearfish observed during annual NMFS/SEFC recreational billfish surveys, 1974–86.

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TABLE 1.—Fishery and biological data of spearfish caught during the annual NMFS/SEFC recreational billfish surveys, 1974–86.

Fisheries parameter	Number caught	Percent (%)
Time		
0600–0800	2	4.8
0801–1000	10	23.8
1001–1200	9	21.4
1201–1400	16	38.1
1401–1600	4	9.5
1601–1800	0	0.0
1801–2000	1	2.4
Total	42	100.0
Bait		
Artificial	12	41.2
Natural (deed)	10	34.5
Combination	7	24.3
Total	29	100.0
Sex		
Male	12	60.0
Female	8	40.0
Total	20	100.0

figures reported by Robins (1975) for recreationally caught spearfish in Florida and are considerably smaller than the reported maximum length of 200 cm and weight of 45 kg (Nakamura 1985). The length:weight relationship of 34 spearfish observed is given in Figure 2. Also, there is no notable sexual dimorphism reflected in the spearfish length-weight relationship (Fig. 2) as reported in other billfish species (Nakamura 1985). This, however, may be an artifact of the small sample size.

The determination of an accurate sex ratio is difficult owing to the small sample size (Table 1) and the large time frame and geographic area from which these data were collected. Of the 20 fish that were reliably sexed, 12 were male and 8 were female; this indicates a male to female ratio of 1:0.66, compared with the 19 specimens and 1:1 ratio observed by Robins (1975) in the Florida recreational billfish fishery. When the two data sets are aggregated to form a larger sample size of recreationally caught spearfish, these data provide a ratio of 1:0.80. Interestingly, Ueyanagi et al. (1970) reported that 106 male and 62 female spearfish were incidentally captured by Japanese tuna longline vessels in the

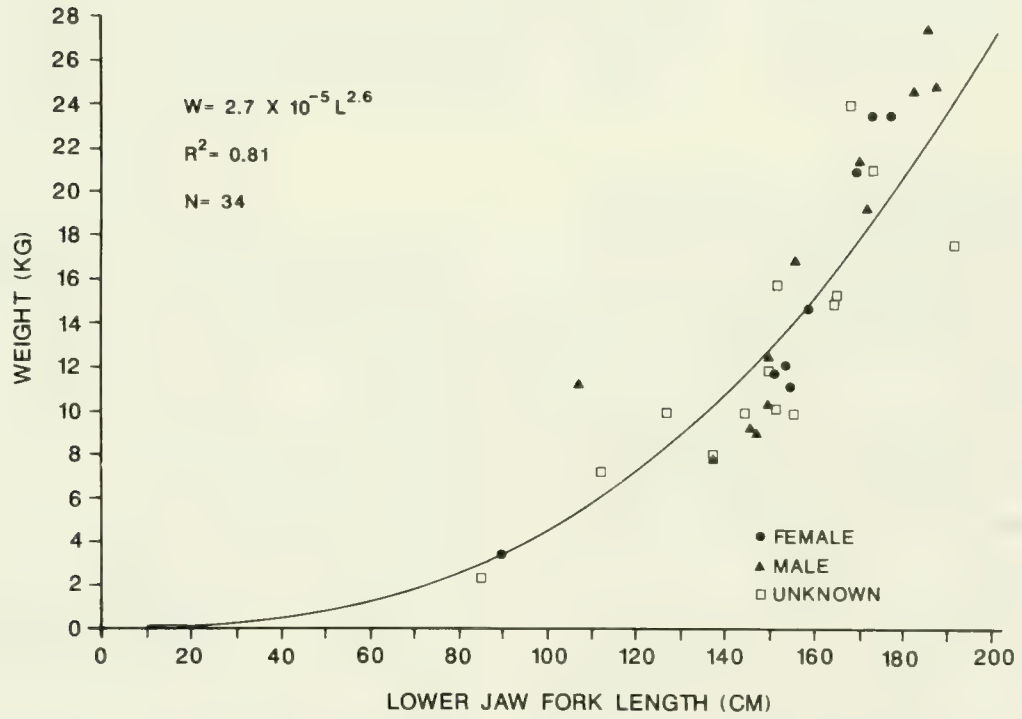

FIGURE 2.—Length:weight relationship of spearfish observed during annual NMFS/SEFC recreational billfish surveys, 1974–86.

western north Atlantic at a ratio of 1:0.58. This suggests that the recreationally derived sex ratios may, in fact, be realistic.

The catch of recreationally caught spearfish varies temporally and spatially (Table 2), with an overall value of 0.00869 fish caught per 100 hours. The Caribbean produced the highest CPUE for spearfish followed by the Gulf of Mexico, the eastern United States, and the Bahamas.

TABLE 2.—Catch and effort (expressed as hours fished) data of spearfish caught during annual NMFS/SEFC recreational billfish surveys, 1974–86.

Year	Gulf of Mexico catch/effort	Eastern U.S. catch/effort	Caribbean catch/effort	Bahamas catch/effort	Total catch/effort	CPUE[1]
1974	1/11,005	0/ 8,728	0/ 3,935	0/ 6,711	1/30,379	0.00329
1975	2/15,060	0/10,949	0/ 3,809	0/ 5,879	2/35,697	0.00560
1976	1/ 8,904	0/ 9,077	0/ 2,844	1/ 5,283	2/26,148	0.00764
1977	3/11,600	0/11,070	0/ 2,473	0/ 5,200	3/30,343	0.00988
1978	9/31,905	1/11,429	0/ 4,156	1/ 5,606	11/53,096	0.02071
1979	3/10,960	0/ 9,351	0/ 676	0/ 6,383	3/27,370	0.01096
1980	0/13,312	2/22,140	0/ 236	0/ 8,041	2/43,729	0.00457
1981	4/15,525	0/16,720	0/ 2,182	1/10,688	5/45,115	0.01108
1982	1/ 8,863	0/ 8,504	0/ 2,251	0/ 9,710	1/29,328	0.00340
1983	0/13,304	2/34,169	6/19,148	0/11,441	8/78,062	0.01024
1984	2/14,524	2/28,520	0/ 9,675	1/16,014	5/68,733	0.00727
1985	1/12,599	0/12,140	1/11,845	0/12,071	2/48,655	0.00411
1986	1/10,604	2/19,204	1/ 3,735	0/13,588	4/47,133	0.00848
Total	28/178,165	9/202,001	8/67,005	4/116,615	49/563,786	0.00869
CPUE	0.01571	0.00445	0.01193	0.00343	0.00869	

[1]CPUE = Number of spearfish caught per 100 hours fished.

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Age Determination in Larval and Juvenile Sheepshead, *Archosargus probatocephalus*

Pannella (1971) first demonstrated the existence of daily growth increments in the otoliths of several species of teleosts. Enumeration of these daily increments is particularly useful for age determination in larval and juvenile fishes. Verification of daily growth rings in individual fish species has generally been approached in one of two ways: laboratory rearing (Brothers et al. 1976; Struhsaker and Uchiyama 1976; Taubert and Cable 1977; Barkman 1978; McGurk 1984; Davis et al. 1985;) or by using chemical marking techniques either in the wild or in the laboratory. Oxytetracycline hydrochloride has been used to produce a fluorescent mark for examination of daily growth increments in otoliths of the starry flounder, *Platichthys stellatus* (Campana and Neilson 1982), and juvenile Hawaiian snapper, *Pristipomoides filamentosus* (Ralston and Miyamoto 1983). Otolith microstructure and its use in fish age determination was reviewed by Campana and Neilson (1985).

The early life history of the sheepshead, *Archosargus probatocephalus*, is poorly known. In this study, daily growth rings in the otoliths of larval and juvenile sheepshead were examined and validation was accomplished using tetracycline-marked specimens held in the laboratory. The daily rings of wild caught specimens were counted to obtain information on the age at transition from larva to juvenile.

Materials and Methods

Sheepshead larvae and juveniles were collected from Bayboro Harbor, St. Petersburg, FL, between 21 April 1983 and 7 May 1985. Larvae (5–8 mm SL) and juveniles (greater than about 8 mm) were collected from a seawall using a dip net fished at the surface. All specimens were preserved in 95% ethanol. Subsamples of larvae were measured (SL) using an ocular micrometer, and the sagittal otoliths were teased out and mounted on microscope slides using Pro-texx[1] mounting media. In the largest individuals (about 10 mm SL), one otolith was mounted on a microscope slide in thermoplastic cement and polished with 3 μ grit microtome paper. The otoliths were polished until the rings near the primordium were clearly visible (Fig. 1).

The daily nature of the growth increments was validated using 29, (7–10 mm SL) wild-caught larvae collected on 1 May 1984. Larvae were placed in 38 L aquaria containing oxytetracycline hydrochloride at a concentration of 10–15 mg/L, left for 7 hours, and then were removed to untreated tanks. Fish were fed *Artemia salina* nauplii and allowed to grow for 6 or 15 days, after which they were preserved in 95% ethyl alcohol and stored in the dark. The position of the tetracycline mark was determined by preparing these otoliths as described above and alternately viewing them under ultraviolet and visible light.

Otoliths were examined at 630–1000× magnification using a compound microscope equipped with a high resolution closed circuit television to improve contrast. Daily growth increments were independently counted by two readers. Counts were considered in agreement if they differed by two or less increments. When the counts differed by two increments, the median value was used; when they differed by one increment, the greater value was used. If counts differed by three or more, those otoliths were reexamined by both readers in a joint effort to resolve the differences. About 5% of the otoliths were excluded from the data set because differences in counts could not be resolved.

Results

Approximately 2,000 larval and juvenile sheepshead, ranging in size from about 5–10 mm, were collected during the study (Fig. 2). About 90% of the individuals were 6.5–8.0 mm (mean = 7.0 mm); fish larger than approximately 8 mm represented less than 2% of the sample. Rings in otoliths of larval and juvenile sheepshead were clear (Fig. 1), and results of the validation experiment confirmed daily increment formation, at least between 7 and 10 mm. Of 26 specimens sacrificed six days after tetracycline treatment, 19 showed clear marks and had produced six increments beyond the reference mark. Reference marks could not be located on six of the remaining specimens, and the increments could not be counted on one specimen. The specimens sacrificed after 15 d post-treatment showed clear reference marks and had produced 15 increments.

A sample of 129 larval and juvenile sheeps-

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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Fishery Bulletin, U.S. 87:985–988, 1989.

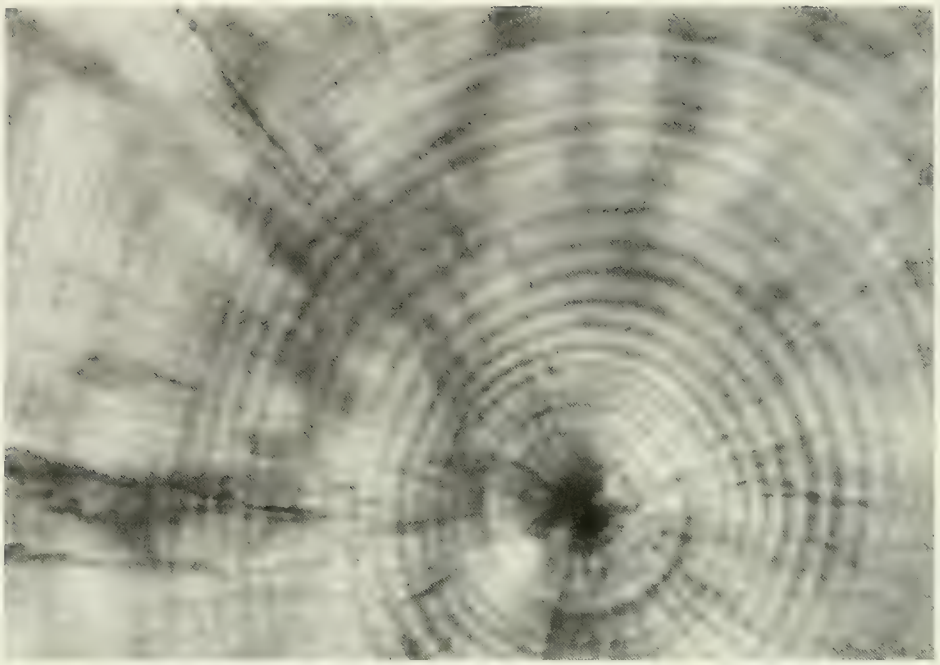

FIGURE 1.—Photomicrograph through the central region of an otolith taken from a 10.5 mm sheepshead (80× magnification). This otolith was polished to increase ring clarity.

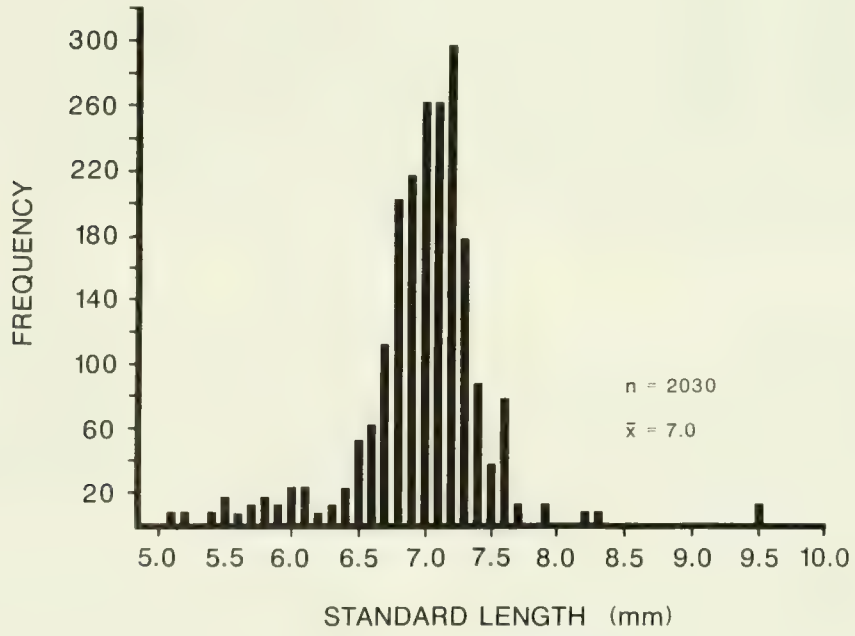

FIGURE 2.—Length-frequency distribution of all sheepshead collected by dip net from the Bayboro Harbor site.

head (5.1–10.5 mm SL) were aged. First increment formation was assumed to begin at hatching such that the otolith age equals the "real" age. Of this sample, 93 specimens were taken from field collections, the remainder were tetracycline treated individuals held in the laboratory. Figure 3 shows the results of these age determinations.

Discussion

Once daily periodicity in increment formation was validated in sheepshead otoliths through the use of tetracycline marking, it was possible to determine the timing of life history transitions. The time required for transition from larval to juvenile stage has been determined for a number of species (Brothers et al. 1983; Campana 1984). The data presented in Figure 2 indicate that by about 8 mm SL most sheepshead larvae have disappeared from dip net collections. This coincides with the size at beginning of transformation as reported by Mook (1977). The disappearance of larvae from collections may reflect their ability to avoid capture or their movement out of the pelagic environment, both facilitated by increased swimming ability acquired after metamorphosis. Sheepshead are substrate-oriented fish, and a "settling" of larvae may occur at metamorphosis. Using the data presented in Figure 3, the minimum and maximum age of an 8 mm fish can be roughly estimated at about 30 and 40 days, respectively. If daily increment formation begins at hatching (see Brothers et al. [1983] for a discussion of this assumption) then the pelagic stage of the sheepshead under the environmental conditions of Bayboro Harbor is between about 30 and 40 days. Other species possessing similar ages/sizes at transition include the spot, *Leiostomus xanthurus*, which transforms at 8 mm after 40 days (Fahay 1983; Warlen and Chester 1985) and the Atlantic croaker, *Micropogonias undulatus*, which transforms at 10 mm after 60 days (Fahay 1983; Joann Lyczkowski-Shultz[2]. The results presented here suggest that sheepshead larvae develop more slowly than the larvae of the closely related sea bream, *Archosargus rhomboidalis*. Sea bream larvae reared in captivity began transformation at the same size as sheepshead (8 mm) but only 15 days after hatching (Houde and Pothoff 1976). It is noteworthy that five sheepshead larvae (7.9–8.1 mm), held in the laboratory during tetracycline treatments, were found to have a mean age of 36.8 days (range = 35–38 days) (Fig. 3). These comparisons must be cautiously interpreted, however, because growth acceleration or retardation may occur in captivity.

Acknowledgments

I would like to thank the employees of the Florida Department of Natural Resources,

[2]J. Lyczkowski-Shultz, Gulf Coast Research Laboratory, P.O. Box 7000, Ocean Springs, MS 39564, pers. commun. March 1989.

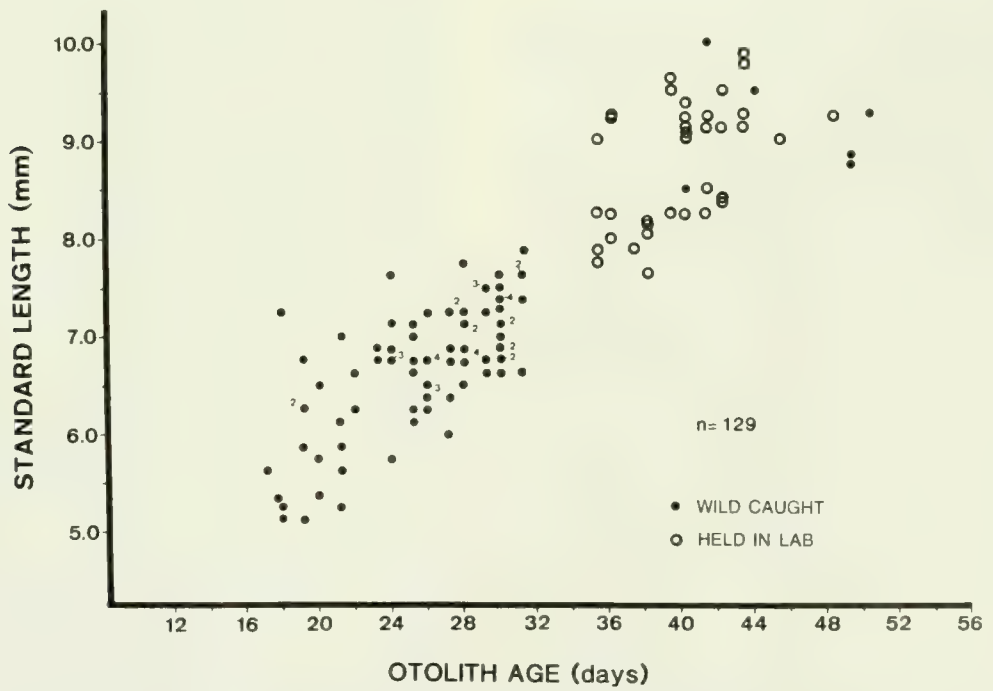

FIGURE 3.—A scatter plot of length on age for larval and early juvenile sheepshead between 5 and 10 mm SL.

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Reproductive Status of Dover Sole, *Microstomus pacificus*, off Northern Oregon

Dover sole, *Microstomus pacificus*, range latitudinally from northern Baja California to the Bering Sea (Hart 1973) but are commercially abundant only from central California to British Columbia. They inhabit a wide depth range, from shallow, inshore waters (juveniles) to at least 1,000 m. Maximum recorded size is 71 cm total length (Hart 1973). On the basis of biomass, Dover sole is the most abundant species of flatfish landed commercially off Oregon (Demory et al.[1]) and dominates the Columbia Slope Assemblage (located at depths >220 m) described by Gabriel and Tyler (1980). Landing and effort statistics for this species in the International North Pacific Fisheries Commission (INPFC) Columbia Area (lat. 43°00′–47°30′N) were relatively stable for the 20 years prior to 1977, but have since almost tripled (Demory et al[2]).

From data extending back to 1951, Demory et al. (fn. 2) suggested a decline in age-specific length for this species during the last several years (mean length at age 10 years was about

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[2]Demory, R. L., J. T. Golden, and E. K. Pikitch. 1984. Status of dover sole (*Microstomus pacificus*) in INPFC Columbia and Vancouver areas in 1984. Unpubl. rep. Oreg. Dep. Fish Wildl., Newport, OR 97365.

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43.5 cm, 42.3 cm, and 38.3 cm in 1951, 1965, and 1982, respectively). Because fecundity is proportional to size, this decline implies that the reproductive capacity of the stock has decreased (Bagenal 1973; Borisov 1979), provided that relative fecundity or size and age at first maturity have not undergone compensatory changes. Data on fecundity and state of maturity of Dover sole off Oregon have not been collected since 1950 (Harry 1959).

In this paper, we describe fecundity of Dover sole from the Columbia area during the 1985–86 spawning season as a function of length, weight, and age, and compare the relationship between length and fecundity with that previously estimated from fish collected between 1948 and 1950 in the same geographical area (Harry 1959). Size and age at maturation are also assessed and compared with the limited information presented by Harry (1959).

Materials and Methods

Samples for estimating fecundity were obtained from commercial trawlers fishing off northern Oregon (about lat. 46°N) during December 1985. Fish total length (TL, nearest mm) was measured and both otoliths were removed and stored in 50% ethanol for age determination. Ovaries were preserved in a 10% phosphate-buffered formaldehyde solution. Maturity stages were assigned using macroscopic inspection of ovaries and oocytes and applying criteria described by Hagerman (1952). Comparable criteria were used by Harry (1956). Because most specimens were filleted prior to sampling, the relationship between total length and ovary-free body weight (nearest 0.1 g) was established from intact fish collected at the same time. Body weight at length for filleted fish was estimated from this relationship. Additional specimens (collected from 44° to 45°N) were sampled in December 1985 and January 1986 from processing plants in Newport, OR and used to describe state of maturity. Total length was measured and otoliths were removed.

Oocyte counts for fecundity estimates were made using the gravimetric subsampling method for MacGregor (1957), as described by Hunter et al. (1985). Both ovaries preserved from each fish were blotted dry and weighed to the nearest 0.1 g. Three subsamples of oocytes were removed from each fish (one each from the anterior, middle, and posterior regions of one ovary, either left or right). Subsamples were weighed to the nearest 0.1 mg, placed on microscope slides in 33% glycerin, and teased apart to form one layer of oocytes. Minimum and maximum diameters of mature, yolked oocytes were estimated from each subsample. Subsamples weighed between 30 and 80 mg, and contained about 100–300 oocytes.

Ovaries were advanced enough to allow discrimination of large, mature oocytes from smaller partially-yolked oocytes and non-yolked oocytes by the unaided eye. Oocyte size-frequency distributions were determined microscopically from the ovaries of 10 fish (MacGregor 1957). Using a Zeiss Videoplan II[3] image analyzer, and a dissecting microscope with camera lucida attachment, approximately 250 oocytes lying along transect lines etched in the microscope slide were measured to the nearest micron, and size-frequency distributions were evaluated. The modal size group of advanced oocytes was determined by visual inspection of the size-frequency plots. An average minimum size-threshold for oocytes associated with the most advanced and distinct modes in these 10 plots was determined. Ovaries with advanced oocytes that all exceeded this size-threshold were used in estimating fecundity. Individual fecundity was calculated by multiplying total ovarian weight by mean number of advanced oocytes per mg in the three subsamples.

Age was determined for each fish used in estimating fecundity and for a subsample of those fish used for maturity assessment. The left otolith was prepared and sectioned as described by Boehlert and Yoklavich (1984). Annuli were counted on a dissecting microscope at 80× magnification using reflected light and a black background. Age was determined twice for each fish, approximately one month apart, to establish precision of the age estimate. There was no difference between the two age determinations for each of 75 fish (paired t-test, $P > 0.50$). The first estimate was used in further analyses. There has been no age validation for Dover sole, but similar methods have accurately aged other long-lived species (*Sebastes diploproa*, Bennett et al. 1982; *A. fimbria*, Beamish et al. 1983; *S. flavidus*, Leaman and Nagtegaal 1987).

Results

To determine fecundity, 97 ovaries were col-

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

lected during the first two weeks of December 1985. Eighteen ovaries were spent, while the others were classified as mature ovaries, full of developing oocytes that were distinguishable by the unaided eye. Fifty-seven of the mature ovaries, from fish 345 to 550 mm TL, were used for fecundity assessment; ovaries of the remaining 22 fish were either poorly preserved or not intact. No hydrated or translucent oocytes were evident in the ovaries used for fecundity. Size-frequency distributions of oocytes from 10 mature, prespawning fish were generally bimodal (Fig. 1). Seven of these ovaries had distinct modes of advanced oocytes; from these

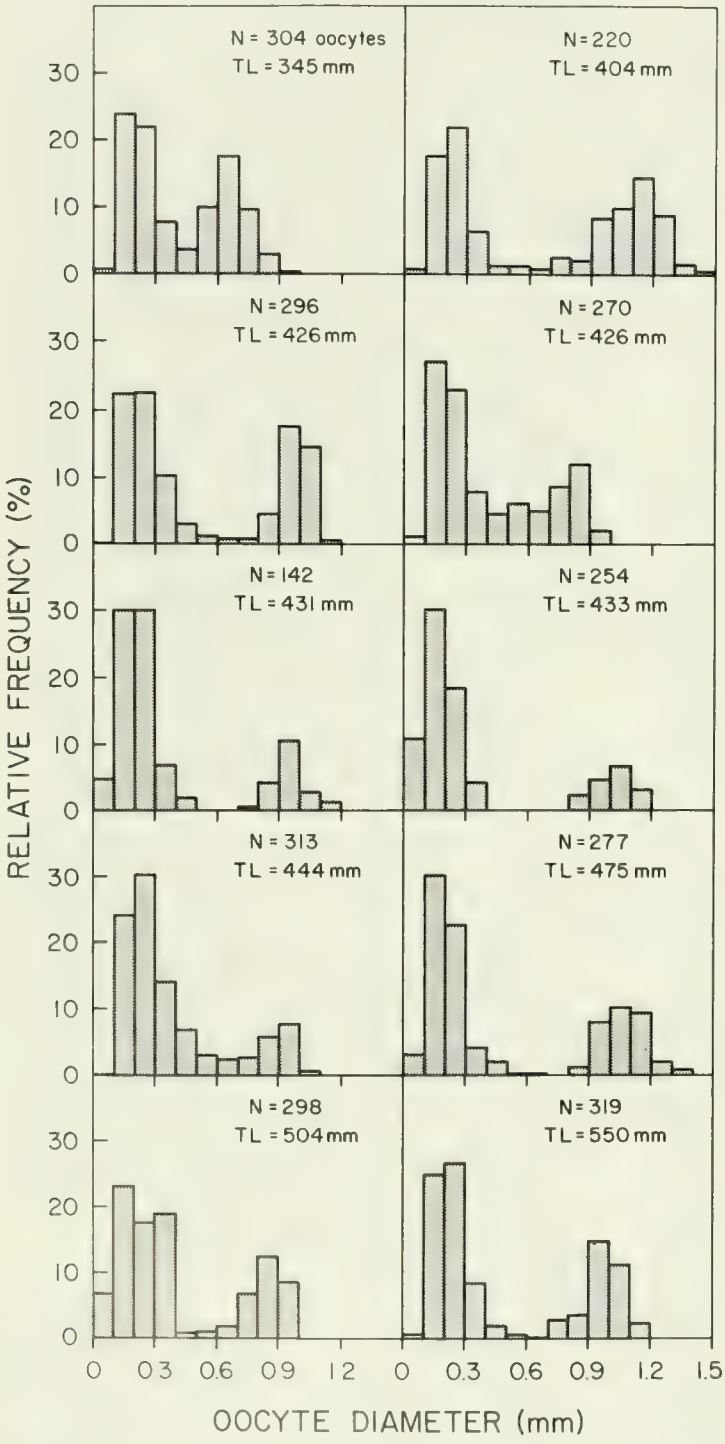

FIGURE 1.—Size-frequency distributions of oocyte diameter from ovaries of 10 Dover sole. Total length of fish and number of measured oocytes are indicated.

distributions, the mean minimum size was 0.65 mm for advanced, yolked oocytes to be used in fecundity estimates. The largest measured oocytes were 1.45 mm in diameter.

The number of advanced, yolked oocytes (≥0.65 mm in diameter) per mg of tissue was calculated for each of three subsamples from 32 of the 57 ovaries. The coefficient of variation ranged from 0.1 to 9.1%, with a mean of 4.0%. This range is comparable to that found when enumerating the eggs of sablefish, *Anoplopoma fimbria*, (Mason et al. 1983) and widow rockfish, *Sebastes entomelas*, (Boehlert et al. 1982).

Fecundity of Dover sole ranged from 39,748 to 167,046 oocytes. As expected, fecundity increased with increasing length of fish (Fig. 2); this relationship was best described by the following power equation, using nonlinear, least squares regression methods:

$$F = (1.637 \times 10^{-6})L^{4.02} \qquad r^2 = 0.82,$$

where F is fecundity (total number of advanced oocytes per fish), L is total length of fish (mm), and r^2 is the coefficient of determination.

We found no statistical difference between the fecundity-length relationship from Dover sole collected by Harry (1959) and those reported here. A linear, least squares regression of our logarithmically transformed length-specific fecundity data was compared with an analogous function we derived from Harry's data, for lengths of fish common to both studies (425–550 mm TL; Fig. 2). Neither slopes (t-test, $P > 0.510$) nor intercepts (t-test, $P > 0.078$) of the regression lines differed significantly. The proportion of the total variation in fecundity that is accounted for by the fitted regression ($r^2 = 0.82$ in the present study and $r^2 = 0.75$ in Harry (1959)) is typical for many species of fish and reflects variable body weight, nutritional condition, age, and possible onset of spawning (Bagenal 1973; Hempel 1979).

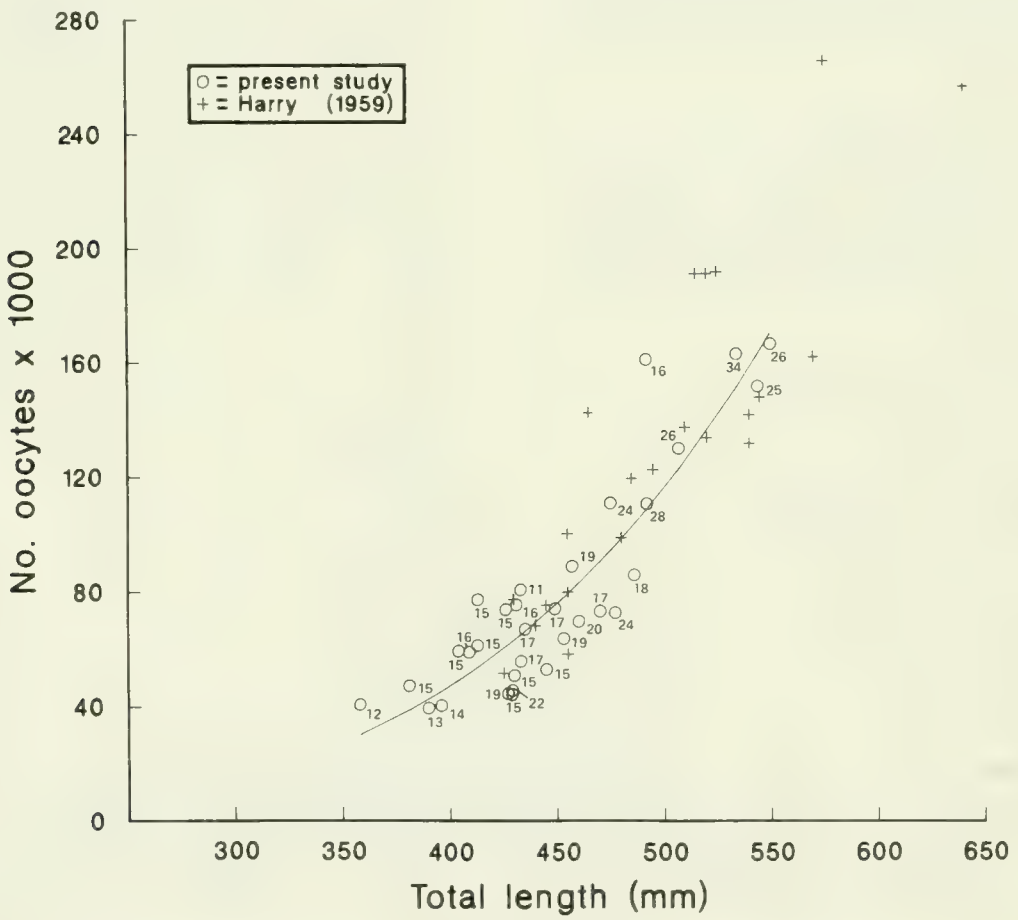

FIGURE 2.—Fecundity of Dover sole relative to total length. Open circles represent fecundity from present study ($N = 32$) and line is the predicted relationship through these points ($F = 1.637 \times 10^{-6}\ L^{4.02}$). Crosses represent fecundity estimated by Harry (1959; $N = 22$). Number adjacent to open circle indicates age of female.

Ovary-free body weight (W; 185–1,490 g) and total body length (L; 287–550 mm) from a sample of 115 female Dover sole were fit with a nonlinear, least squares power function:

$$W = (3.34 \times 10^{-6})L^{3.147} \qquad r^2 = 0.96.$$

Ovary-free body weight was subsequently estimated from total length for those Dover sole that were filleted prior to sampling. Fecundity was expressed as a linear, least squares function of ovary-free body weight, resulting in the fitted equation:

$$F = 133.4W - 21{,}890.3 \qquad r^2 = 0.81$$
$$N = 32,$$

where N is number of ovaries. Although weight was estimated from total length of fish, this fitted equation is adequate because the variance of errors associated with estimated weight is very small when compared with the variance in the weights themselves (Draper and Smith 1981, p. 124). Weight-specific fecundity averaged 102.4 eggs/g ovary-free body weight (SD = 22.0, N = 32).

The Dover sole used for determining fecundity were 11–34 years of age. Fecundity and age were not as strongly correlated as fecundity and length or weight, yet fecundity generally increased with increasing age (Fig. 2). The relationship between fecundity and age, from the 32 fish evaluated in this study, was best fit by a nonlinear, least squares exponential function:

$$F = 25{,}080\, e^{(0.0586A)} \qquad r^2 = 0.65,$$

where A is age of the fish in years.

Stage of maturity was determined for 370 female Dover sole, ranging in size from 235 to 489 mm TL (Fig. 3). Because samples were collected from processing plants, many small fish had been discarded at sea and were poorly represented. Emphasis was placed on obtaining information from fish below fillet size (320 mm TL). Nearly 99% of the fish examined were classified as sexually mature; 67.2% of these were spent, and 32.5% contained ovaries with advanced, yolked oocytes that were clearly discernible upon macroscopic inspection. Only four fish (305–318 mm TL) were immature, and one fish was in a resting stage. Advanced oocytes occurred in fish of all lengths. This relationship suggests that fish were maturing at a much smaller size than that reported by Harry (1959; Fig. 3). State of maturity seems to be dependent on the size of the fish. Frequencies of fish in five 5 cm length groups (24–28; 29–33; 34–38; 39–43; and 44–48 cm) and in two states of maturity (advanced oocytes and spent ovaries) were arranged in a 2 × 5 contingency table; the independence of total length and state of maturity was tested. Significantly more of the small fish were spent (Chi-square = 78.76; $P <$

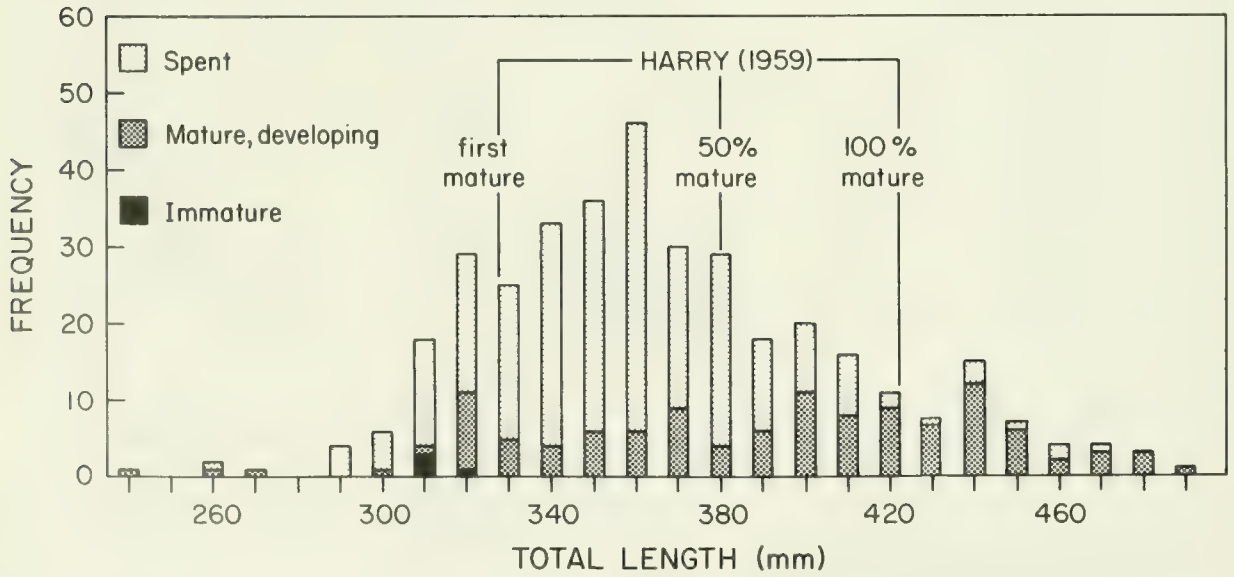

FIGURE 3.—Length frequency of 370 female Dover sole at three stages of maturity. Comparative information from Harry (1959) is indicated.

0.001); smaller fish appear to have an earlier, and possibly shorter, spawning season. Preliminary data on Dover sole collected in California indicated that larger fish still contained eggs in late spring (Hunter[4]), thus supporting our findings.

From those fish assessed for state of maturity, a subsample of 162 was selected for age determination. All were mature; 78% were spent, and 22% contained advanced, yolked oocytes. Fish were 5–24 years old (Fig. 4). As expected from the length at maturity analysis, most (77.1%) of the 35 fish with advanced oocytes were older than 10 years of age; 53.5% of the spent fish were older than 10 years.

Discussion

One cannot conclude unequivocally that the estimated number of advanced oocytes prior to spawning corresponds to reproductive output of Dover sole, owing to incomplete spawning events or resorption of oocytes (Foucher and Beamish 1980). In addition, considering that 20% of the females collected for fecundity estimates during December were spent, some fish with advanced ovaries may have partially spawned. If so, fecundity would have been underestimated for those fish. We maintain that our data reflect the potential fecundity of Dover sole for the following reasons: 1) oocyte size distributions did not demonstrate a distinct spawning batch (oocyte diameter >1.80 mm), suggesting that these females had not yet spawned; 2) no hydrated oocytes were observed in the ovaries used for fecundity estimates, although hydration could occur rapidly and therefore its absence could be a sampling artifact; and 3) our coefficients of determination for regressions of fecundity on length and on weight are relatively high ($r^2 = 0.82$ and 0.81, respectively); if a significant number of oocytes had been released, variability could have conceivably been much greater. An additional source of underestimation

[4]J. Hunter, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA, 92038, pers. commun. June 1986.

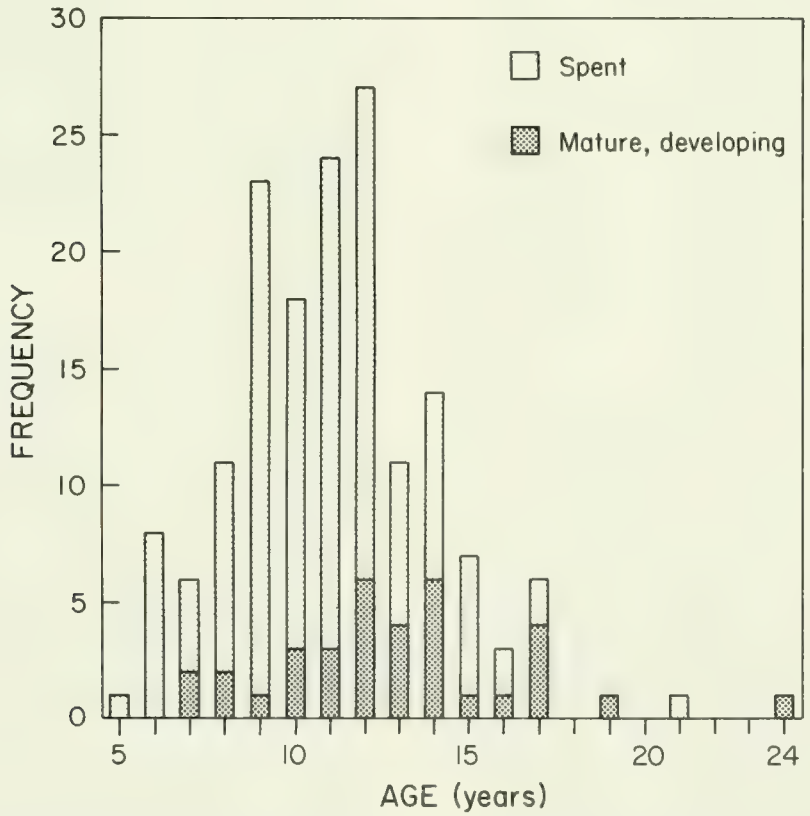

FIGURE 4.—Age-frequency distribution of 162 female Dover sole, classified as either mature with advanced oocytes, or mature and spent.

concerns the small, partially-yolked oocytes (<0.65 mm) that potentially could be recruited to the advanced mode but were excluded from fecundity estimates. Using the average lower limit of advanced oocyte diameters (from only those seven ovaries with clearly separated, advanced modes) as the minimum size of oocytes destined for release, it was assumed that further contribution of smaller oocytes would be unlikely and minimal in the current season.

A compensatory increase in fecundity following a reduction in population density was suggested by Bagenal (1973). We did not detect significant changes in length-specific fecundity for Dover sole despite tripled landings and the suggested decrease in age-specific length since 1977 (Demory et al., fn. 2). However, a decline in reproductive output is unlikely because our data indicate a compensatory shift in size at first maturity. Dover sole now mature at significantly smaller sizes than reported by Harry (1959). We found all fish >320 mm to be mature (the smallest mature fish was 240 mm). Although only 15% (or 245 specimens) of those fish in Harry's study were smaller than 380 mm, they were 330 mm at first maturity, 380 mm when 50% mature, and 420 mm when 100% mature (Fig. 3). Similar sizes at maturity were reported by Hagerman (1952) for Dover sole collected in northern California in 1949. The 45 females (5% of total sample) <330 mm were all immature.

The evident change in size at maturity during the interim 35 years may reflect differences in the criteria used for assessing stage of maturity, and in the time of year and size of the fish used for maturity assessments. Harry collected samples between May and October, which excludes the peak spawning months of December and January. Postspawning, inactive, mature ovaries are difficult to differentiate from immature ones during the early summer months using anatomical or histological criteria (Hunter, fn. 4). Classifying postspawners as immature would lead to a greater size at 50% maturity than that estimated from samples collected within the peak spawning period. Size at first maturity, however, should be relatively independent of season, since it seems unlikely that stage of maturity would be incorrectly identified in all smaller fish. Also, as egg development becomes more evident with the approach of spawning season, the mature ovaries become easier to identify (at least in Harry's August–October samples). Despite these potential problems with data comparisons, a decrease in length at maturity is clear and supported by evidence that Dover sole ≥370 mm collected in the Columbia area during the 1980–81 spawning season were all mature (Demory et al., fn. 2).

We cannot assess possible changes in the age-maturity relationship, because comparable ageing methodology was not used by Harry (1959). It cannot be inferred, however, that Dover sole are maturing at younger ages concurrently with smaller sizes, because length at age has also declined.

Although the decrease in length at maturity implies that individual reproductive potential is improved, lack of historical information on accurate age-specific maturity and fecundity makes it impossible to detect any net change in reproductive output per individual. To identify changes in the reproductive output of the Dover sole off Oregon, a reliable assessment of spawning biomass, size and age structure of the population, and both length and age at maturity is required.

Increased landings and effort may have affected the duration and timing of the spawning season, which could influence year class strength. Size-selective exploitation removes relatively more of the larger and older Dover sole (Best 1961). Larger individuals are not only more fecund, but appear to have a longer and/or later spawning period than small, young fish. The reproductive status and population dynamics of Dover sole, as influenced by factors discussed here, can be further understood with continued, appropriate, long-term research.

Acknowledgments

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Digestive-Gland Histology in Paralarval Squids (Cephalopoda: Loliginidae).

The transition from hatchling to adult in cephalopods does not involve a radical metamorphosis as is found in many other marine invertebrates (Boletzky 1974), but distinctive changes occur early in development (Vecchione 1979, 1981, 1982), similar to those found in fishes. The highest, and perhaps the most variable, rates of prespawning mortality in cephalopods occur during this paralarval development. A recent review of the early life history of cephalopods (Vecchione 1987) presented evidence that starvation, resulting from failure to feed successfully after absorption of the internal yolk, may be a major cause of paralarval mortality. However, other explanations, such as predation or suboptimal environmental conditions, may also explain high paralarval mortality rates. To test among these alternatives, methods must be developed to determine whether paralarval squids are suffering from starvation.

Similar problems exist in ichthyoplankton

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ecology. Histology has been used to determine whether larval fishes are starving at sea (O'Connell 1976, 1980; Theilacker 1978, 1986; Govoni 1980; Eldridge et al. 1981; Kashuba and Matthews 1984). In cephalopods, the digestive gland is uniquely suited to be a target for a histological study of feeding history. The cells of the digestive gland can be categorized along a developmental continuum of immature, synthesizing, mature, and resting cells of a single type (Boucaud-Camou and Yim 1980; Boucaud-Camou and Boucher-Rodoni 1983; Boucher-Rodoni et al. 1987). Boucher-Rodoni et al. (1987) proposed that the developmental condition of the cells of the digestive glands of very young *Sepia officinalis* and other cephalopod paralarvae could be used as an indicator of successful first-feeding.

The digestive-gland cells in the genus *Loligo* undergo a developmental sequence similar to that of other cephalopods (Portmann and Bidder 1928), although Boucher-Rodoni and Boucaud-Camou (in press) have found that the digestive gland in *Loligo* differs substantially from that of other cephalopods. The cells of the loliginid digestive gland are characterized by large apical vacuoles containing lipids and carbohydrates (Bidder 1950, 1966).

We examined the digestive glands of paralarval *Loligo*, both *L. pealei* from field collections and *L. forbesi* that had been hatched and maintained in the laboratory under known nutritional conditions. Specifically, we wanted to see whether the presence of mature digestive-gland cells could be associated with successful first-feeding in the commercially important squid family Loliginidae.

Materials and Methods

Laboratory squids were obtained from an experiment in culturing the eastern Atlantic species *Loligo forbesi* (Hanlon et al. 1985). Because the primary objective of the experiment was to determine methods for successfully culturing squids, the squids could not be sacrificed on an optimum schedule for determination of starvation. Furthermore, because the scope of the feeding experiments was limited, the sample available to us (other investigators were interested in other problems) was quite small.

These squids included hatchlings (<1 d old), some of which had been offered zooplankton as food and some that had been kept without food. Also included were squids >1 wk old. These older squids had survived past the point at which death from starvation normally occurs in unfed squids. Among these older squids were some that had been offered zooplankton as food and some that had been kept without food in a seawater culture medium containing a high concentration (10 mg C per L) of dissolved organic material (DOM). Squids collected in the field were *Loligo pealei* sorted from zooplankton samples from the western North Atlantic. The *L. pealei* were chosen to represent the entire paralarval size range (Vecchione 1981) (Table 1).

TABLE 1.—Paralarval squids examined for digestive-gland histology. DOM = Dissolved Organic Material.

Loligo pealei Dorsal mantle length	*Loligo forbesi* Dorsal mantle length	Age	Treatment
2.0 mm	3.8 mm	<1 day	nonfed
2.0 mm	4.1 mm	<1 day	nonfed
2.6 mm	3.3 mm	<1 day	fed
3.0 mm	3.9 mm	<1 day	fed
3.4 mm	3.4 mm	>1 week	fed
5.1 mm	4.0 mm	>1 week	fed
6.4 mm	4.2 mm	>1 week	DOM
6.9 mm	4.4 mm	>1 week	DOM

The field-collected squids were fixed and preserved in 4% formaldehyde in seawater, whereas those cultured in the laboratory were fixed in Bouin's solution and sectioned shortly after fixation. For all squids, 10 μm horizontal sections were prepared after having been embedded in paraffin. Sections were cleared with oil of wintergreen and stained with hematoxylin and eosin. Observations were standardized by selecting sections that, as much as possible, were ventral to the posterior salivary gland and dorsal to the ink sac, although in some squids these organs overlapped dorsoventrally.

Results

Some mature cells containing conspicuous apical vacuoles were found in all squids. Numbers and sizes of vacoules varied as did the relative volume of the glandular epithelium of the digestive gland.

Hatchlings of *L. forbesi* were all similar in appearance, both nonfed (Fig. 1A) and those that had been offered food and therefore may have fed (Fig. 1B, C). The digestive glands appeared to be robust, with thick glandular epithelium that occupied more volume than the

lumen. Numerous small vacuoles were seen throughout the tissue of both the fed and the nonfed squids. Thus, a large percentage of the cells of squids from both treatments could be considered to be mature. Additionally, a few medium-sized and large vacuoles were found in the nonfed hatchlings (Fig. 1A).

The greatest differences between feeding-treatments were found in the *L. forbesi* that had survived for more than 1 week. The digestive-gland tissue of the squids that had been offered zooplankton, and presumably had fed because of their longevity, consisted of thin walls with many long, thin lamellae that extended into a very large lumen (Fig. 2A, B). The volume of the lumen was much greater than that of the digestive-gland tissue. This tissue was characterized by vacuoles that were few but very large (Fig. 2B). Conversely, the digestive glands of the squids that had been raised on DOM had grown but had retained an overall appearance very similar to that of the hatchlings. Digestive-gland tissue was massive, occupying much more volume than the lumen; furthermore, it was

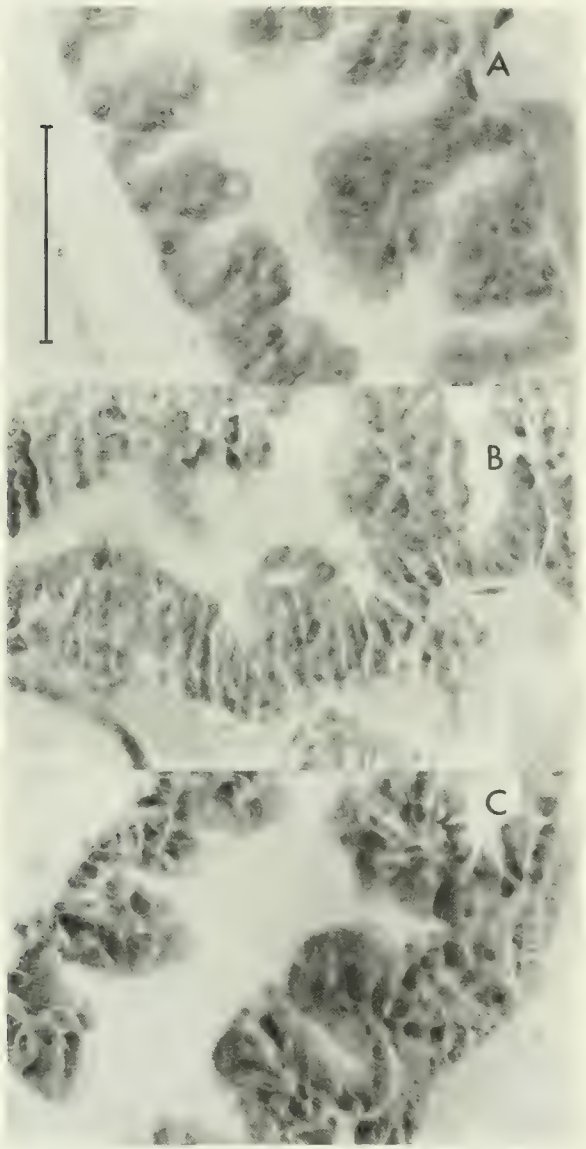

FIGURE 1.—Laboratory-hatched *Loligo forbesi*, < 1 day old: A, 3.8 mm dorsal mantle length (DML), nonfed; B, 3.3 mm DML, from a container with zooplankton food organisms present; C, 3.9 mm DML, from a container with zooplankton food organisms present. Scale bar = 100 μm.

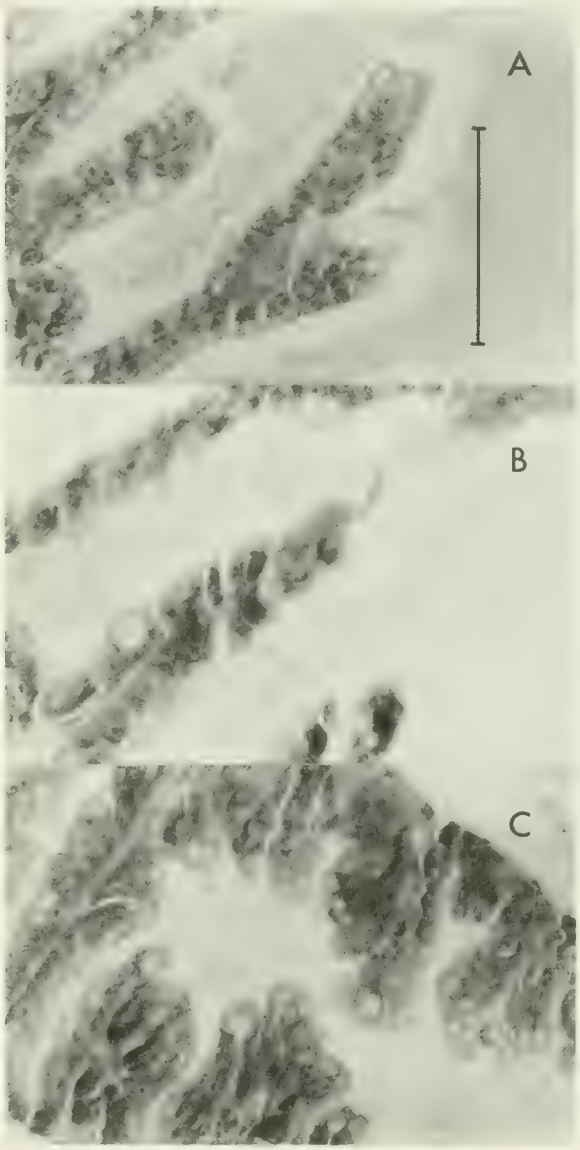

FIGURE 2.—Laboratory-reared *Loligo forbesi*, > 1 week old: A, 3.4 mm dorsal mantle length (DML), fed; B, 4.0 mm DML, fed; C, 4.2 mm DML, from a container with elevated concentrations of dissolved organic matter. Scale bar = 100 μm.

characterized by numerous small to medium-sized vacuoles (Fig. 2C).

Differences between feeding-treatments in the gross morphology of the digestive gland were dramatic (Fig. 3). The digestive glands of squids that had been raised on zooplankton were thin-walled, with large fluid-filled lumina traversed by thin lamellae (Fig. 3A). The digestive glands of squids raised on DOM (Fig. 3B) appeared to be much more robust and well developed, with thick tissue and many small tubules.

Numerous small-to-large vacuoles were found in even the smallest of the field-collected *L. pealei* (Fig. 4A). Digestive-gland tissue was thick, although a large central lumen was present. The internal yolk sac remained in one squid of 2.0 mm dorsal mantle length (DML). In larger *L. pealei* (Fig. 4B, C), vacuoles were numerous and of various sizes but the digestive-gland tissue varied in thickness. In the largest squids examined, tissue growth had filled most of the lumen so that it was characterized by many smaller tubules, similar to those in Figure 4C. These larger paralarvae had few vacuoles but those present were large.

Discussion

Whereas *L. forbesi* has large hatchlings that can be reared in the laboratory (Hanlon et al. 1985), paralarval *L. forbesi* are seldom collected

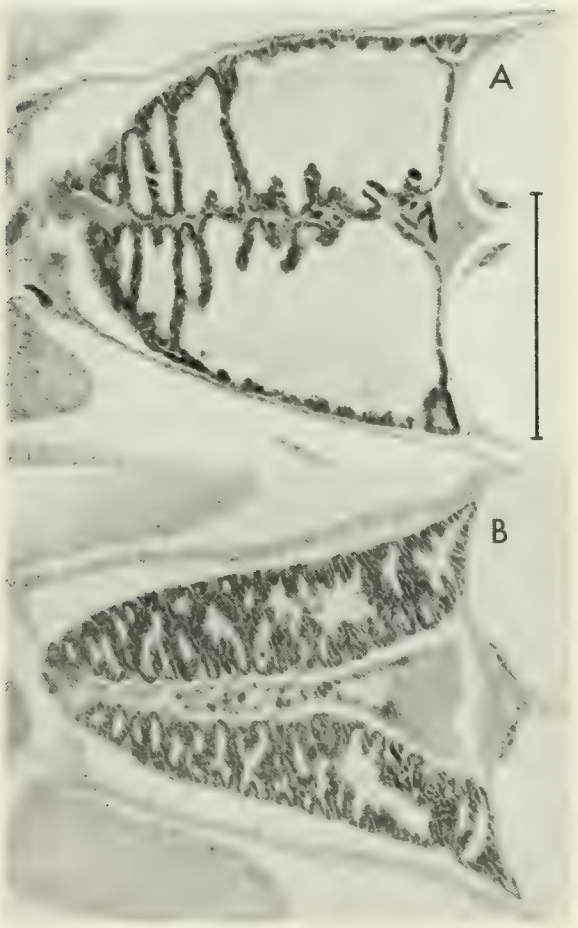

FIGURE 3.—Digestive glands of laboratory-reared *Loligo forbesi*, > 1 week old: A, 4.0 mm DML, from a container with zooplankton food organisms present; B, 4.2 mm DML, from a container with elevated concentrations of dissolved organic matter. Scale bar = 500 μm.

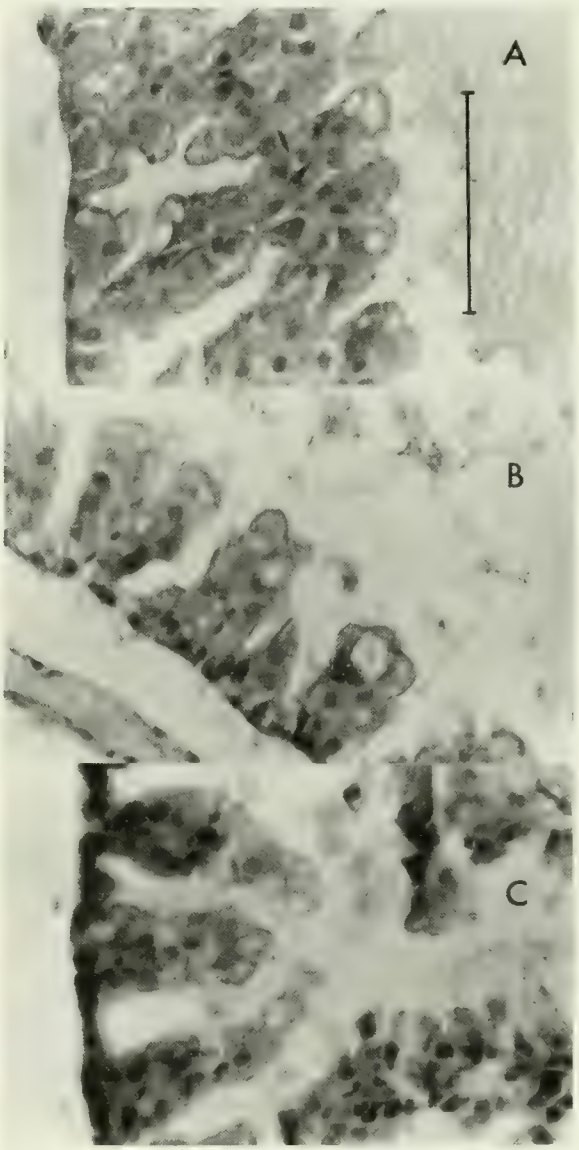

FIGURE 4.—Field-collected *Loligo pealei* paralarvae: A, 2.0 mm dorsal mantle length (DML); B, 3.0 mm DML; C, 3.4 mm DML. Scale bar = 100 μm.

in plankton samples (Holme 1974). *Loligo pealei*, however, is commonly collected in the field (Vecchione 1981), but hatches at a much smaller size and is difficult to rear in the laboratory, suffering at least 99% mortality in the first few days, presumably from starvation (Hanlon et al. 1987). The former species, therefore, was used for laboratory studies and the latter for field observations, even though extrapolation from one species to another must be approached with caution.

The *L. forbesi* hatchlings (< 1 d old) that had not been offered food had unquestionably not fed, but their digestive glands contained many mature cells with conspicuous apical vacuoles. Therefore, the presence or absence of vacuoles is not an adequate indicator of successful first-feeding in this species. Even in *Sepia*, there were indications from tissue-culture experiments that digestive-gland cells may mature slowly in unfed hatchlings (Boucher-Rodoni et al. 1987). Similarly, the large vacuoles cannot be taken as an indication of having fed because the unfed hatchlings had large vacuoles as did the older *L. forbesi* that had been fed and had survived for more than 1 week.

Hatchlings <1 d old that had been offered food may or may not have fed. However, unfed hatchlings typically die, presumably from starvation because the internal yolk sac has been absorbed, within 5 days after hatching. Therefore, the older *L. forbesi* (>1 wk old) that had been offered food probably had fed, although no observations were available to indicate the number of hours or days between their final meal and their time of death and fixation.

Culturing experiments have indicated that elevated concentrations of DOM enhance survival of paralarval *L. forbesi* (P. G. Lee[1]). Thus, the squids from the DOM experiment, while not having fed in the typical sense, had grown and, therefore, were not necessarily starving. The DOM added was a complete diet formulation and would have provided all necessary acids. Approximately 50% of the paralarvae in the DOM experiment survived for 10 days after hatching. Ten of 184 paralarvae from the DOM experiment lived for 12 days, before the experiment was terminated because of an intense bacterial bloom (P. G. Lee[2]). Throughout that period, mortality was higher for paralarvae that had been offered food than for those cultured on elevated DOM.

Digestive-gland structure in the older *L. forbesi* that had been fed was distinctly different from those raised on DOM. Whereas the fed squids had a few very large vacuoles, the DOM squids had very many smaller vacuoles. As noted above, the large vacuoles cannot be taken as an indication of having fed because the unfed hatchlings also had similarly large vacuoles. Furthermore, digestive-gland tissue was very thin on the fed squids compared with those from either the DOM experiment or the field-collected *L. pealei*. It is possible that the fed paralarvae had fed enough to survive beyond yolk absorption but not enough to be completely healthy.

Alternatively, it is possible that the distended lumina and the large vacuoles of the older, fed squids may have been caused by alimentary fluid reaching the digestive gland and entering the cell by phagocytosis for intracellular digestion. If this was the case, the squids raised on DOM simply would have retained immature digestive gland morphology and histology. However, because the field-collected squids, especially the larger ones, were similar in digestive gland structure to those raised on DOM, it seems likely that this is the normal, well-nourished condition. Furthermore, the digestive glands of the field-collected squids and those raised on DOM are both similar in structure to the adult condition (c.f. Boucher-Rodoni and Boucaud-Camou, in press). In the largest field-collected squids, which undoubtedly had passed first feeding successfully, the lumen was largely filled by tissue growth, transforming it into a series of many small tubules. If thin walls of the digestive gland are indicative of poor feeding, none of the field-collected squids showed this indication.

In conclusion, we are not certain which condition (thin tissue with a few large vacuoles or thicker tissue with many smaller vacuoles) is the healthier state. However, we believe that it is likely that the condition of thick tissue with many small vacuoles and reduced lumina, found in the DOM and field-collected squids and similar to the adult condition, represents the healthy, well-nourished condition. The differences in gross morphology between these two conditions are obvious even in cursory examination of sections of the digestive glands of paralarvae. This characteristic may therefore be useful for deter-

[1]P. G. Lee, University of Texas Marine Biomedical Institute, Galveston, TX, pers. commun. 1986.

[2]P. G. Lee, University of Texas Marine Biomedical Institute, Galveston, TX, pers. commun. 1987.

mining the nutritional condition of paralarval loliginids.

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Identification of Habitat of Juvenile Snappers in Hawaii

Deepwater snappers have high commercial and recreational value throughout the tropics, and their fisheries and species biology have been widely studied. However, little is known about the ecology of the juveniles between settlement to the demersal habitat and recruitment to the adult population (Munro 1987). In Hawaii, no information regarding location, size, or habitat of juvenile lutjanids has emerged after more than a decade of concentrated studies of adult stocks (Ralston 1980; Humphreys 1986). The absence of observations and collections of juvenile lutjanids or of their occurrence as prey items in the adult habitat suggests that they settle elsewhere prior to recruitment.

Adult snappers have been frequently reported as being associated with structural relief at depths of 100–500 m (Parrish 1987). In contrast, juveniles have not been caught or visually observed in such habitats in surveys made with scuba or submersible vehicles (Ralston et al. 1986; Moffitt et al. 1989). Owing to the lack of conventional scientific evidence about the habitat of juveniles, occasional reports of juveniles captured by shallow-water recreational fishermen in Hawaii continued to go largely unnoticed by researchers until one angler brought back live juvenile specimens of both *Pristipomoides filamentosus* and *Aprion virescens* in September 1988. This tangible evidence provided the stimulus to conduct some exploratory fishing in relatively shallow waters and to attempt to visually observe the fishes' habitat. This report summarizes the results of that investigation.

Methods

During October 1988, the bottom was fished and observed with scuba at three stations off the eastern side of the Hawaiian Island of Oahu. Stations 1 and 2, separated by 2 km along the coast, were situated outside the barrier reef and between the two main entrance channels of Kaneohe Bay; station 3 was located southeast of Mokapu Peninsula in Kailua Bay (Fig. 1). Most fishing was done in midmorning (0800–1200). At station 3, one afternoon and evening sampling was taken in addition to the morning sampling.

A single day of intensive fishing was done at each station from a small boat with two lines, each bearing three No. 10 circle hooks baited with live shrimp. Fishing was limited to depths of 31–76 m, to allow observation of habitat by scuba. At each station, the boat drifted or occupied sequential, anchored positions along a transect across the bottom contours while the fishing lines were bounced off the bottom. The depth was measured periodically during fishing and immediately following the landing of juvenile bottom fishes.

Habitat observations with scuba were performed at the three stations on mornings soon after the sampling was completed, at the locations and depths where target species had been caught earlier. Fishing with a single line helped confirm observation locations on two occasions: target species were landed immediately before or during the dive. At least two dives were made at each station, one or more in shallow (40–50 m) and the other in deep (51–76 m) water. At stations yielding no fish in either depth range, observations were conducted at depths similar to those yielding fish at the other stations. With the exception of the 52 m dive at station 2, dives in the deep ends of the transects occurred at what proved to be the most productive fishing depths (>61 m). Restricted bottom time at these depths limited diving activities to observing habitat and scanning an area of about 6,000 m^2 for target species.

Additional specimens were concurrently collected from waters off Lahilahi Point on western Oahu by the same methods, except that artificial bait was used on a single line and depth was only estimated (60–90 m) by the amount of line deployed. Stomachs and hindguts of *P. filamentosus* from all sources were examined, and prey items were counted and roughly classified. The *P. filamentosus* containing food items were used in the analysis of occurrence (prey type as a percentage of all individuals eaten) and frequency (percentage of fish containing each prey type).

Results and Discussion

A total of 36 juvenile lutjanids were collected from the three stations (Table 1). *Pristipomoides filamentosus* (n = 30) were caught at all three stations, all at 61–73 m depths; 25 were captured at station 1. Five *Aprion virescens* and the one *Aphareus rutilans* were taken at station 2 at 40 m. At stations 1 and 2, the catch rate consistently declined at all depths in the late morning hours. At station 3, no fish were caught until dusk, when four *P. filamentosus* were

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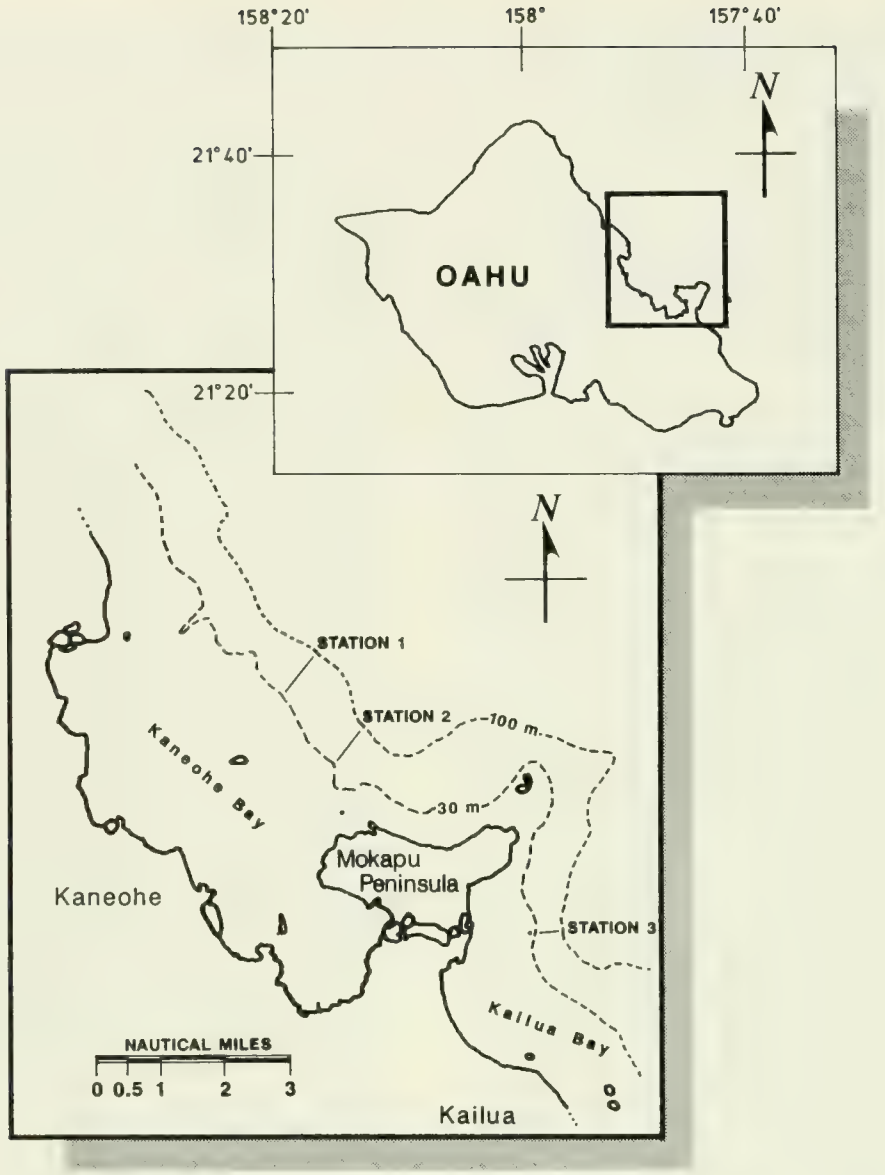

FIGURE 1.—Locations of the three established east Oahu stations.

taken. The west Oahu site yielded seven more *P. filamentosus* for analysis. These results suggest a possible minimum depth of about 61 m for juvenile *P. filamentosus* at the sampled sites.

The scuba observations indicated that the habitat was generally similar at all three stations, but the substrate within each station varied with depth. At the shallow end, the bottom was hard, flat, and devoid of vertical relief. A thin veneer of sand was present, with stands of live *Halimeda* algae evenly distributed over the bottom. Infrequent, shallow depressions in the bottom provided the only substantial relief in which newly settled reef fish (e.g., Pomacentridae and Labridae) were aggregated. No juvenile lutjanids were sighted at this shallow habitat at any of the three stations, although during observation of the habitat at station 2, two *Aprion virescens* were hooked.

The bottom habitats observed at the deep ends of stations 1 and 3, where nearly all the *Pristipomoides filamentosus* were caught, were also similar. The bottom was flat and almost completely devoid of any relief other than minor features produced by sparse benthic biota. The substrate consisted entirely of soft, deep sediment heavily penetrated by burrowing invertebrates. Although no fish were seen during these deep dives, their presence was established at station 1 by the capture of a single *P. filamen-*

TABLE 1.—Results from sampling at three stations on the eastern side of Oahu and at a supplementary site off west Oahu. Numbers in parentheses indicate the actual dive depths (in meters).

Species caught	Depth (m)	Bottom substrate by depth range	
		40–50 m	51–76 m
Station 1			
25 *Pristipomoides filamentosus*	61–73	Hard, flat, with *Halimeda* algae (43)	Flat, soft, fine sediment with invertebrate burrows (69)
Station 2			
5 *Aprion virescens*	40	Hard, flat, with *Halimeda* algae (40)	Flat, coarse sand, without fine sediment (52)
1 *Aphareus rutilans*	40		
1 *P. filamentosus*	67		
Station 3			
4 *P. filamentosus*	67	Hard, flat, without *Halimeda* algae (43)	Flat, soft, fine sediment with invertebrate burrows (70)
West Oahu			
7 *P. filamentosus*	>61		
1 *Aprion virescens*	>61		

tosus at anchor just prior to the dive. At station 2, a somewhat shallower (52 m) dive revealed a substrate consisting entirely of soft *Halimeda* sand without invertebrate burrows or visible fine sediment. After the bottom observations, additional fishing at >61 m depths yielded a single *P. filamentosus*.

Since the density of juvenile lutjanids was probably not great at any location, it is not surprising that they were never sighted by divers. Avoidance behavior by the juveniles may have contributed to the lack of sightings. Our impressions of the habitat based on dive observations were consistent with those from other surveys of the study area (Smith et al. 1973; Coulbourn et al. 1988).

The portion of the life cycle during which juveniles occupy the observed habitat remains unknown. Fork lengths (FL's) of the collected *P. filamentosus* (n = 32) ranged from 10.1 to 20.7 cm; most individuals were clumped at the low end of the range. Planktonic individuals as large as 5 cm have been recorded for a somewhat smaller species, *P. sieboldii*, by Leis (1987). Until the present study, the smallest recorded *P. filamentosus* was 18 cm FL, caught by handline during sampling for adults (Ralston 1981). Using Ralston and Miyamoto's (1983) estimated growth curve derived from adult specimens, a fish of 18 cm FL would be approximately 1 yr old.

Larger identifiable prey items recovered from the stomachs of 22 juvenile specimens of *P. filamentosus* included early juvenile fish (probably recently settled) and cephalopods (including an octopod) (Table 2). The hindgut contained small planktonic crustaceans, appendicularians, and other gelatinous plankton. Most prey individuals were small, but the general taxonomic composition of the diet of the juveniles did not appear greatly different from that of adults. Crustaceans and salps commonly occur in the diet of adult *P. filamentosus* (Kami 1973; Parrish 1987).

TABLE 2.—Approximate percentage of number and frequency of identifiable prey items found in *Pristipomoides filamentosus* juveniles (n = 22).

Prey type	Percent occurrence	Percent frequency
Juvenile fish	2	18
Fish scale	3	18
Small crustaceans	90	72
Cephalopods	2	9
Gelatinous plankton	3	18

Relatively flat, soft bottoms such as occur at these stations have been largely ignored as potentially important habitat for these deepwater lutjanids, but they may provide essential habitat for the juveniles. Artificial structures placed in depths of 61–117 m in Hawaii successfully aggregated deepwater lutjanid adults, but

failed completely to attract juveniles (Moffitt et al. 1989). Although there is little evidence that juveniles avoid such high relief features, there is no evidence of positive association. The limited gut samples from our juveniles did not indicate any material endemic to hard substrate (e.g., coral; obligate, hard bottom-associated invertebrates). Association with structural relief or even with adult bottom fish may put juveniles at risk (Johannes 1978). For example, predators may routinely visit high structural features. Thus, juveniles may pass their early settled life on flat, soft, featureless bottoms. The use of special habitats by prerecruits to avoid competition and possible predation has been observed in both temperate (Carlson and Haight 1976) and tropical fishes (Shapiro 1987). Juvenile lutjanids may also occur on hard, flat bottoms with some limited degree of relief. No fishing on such bottoms was attempted, and extensive sampling effort would be required to eliminate the possibility that such habitat is used.

This brief, preliminary investigation has demonstrated only the presence of juveniles of recreationally and commercially important lutjanids in habitat relatively close to the fishing grounds for adults, but not where adults congregate. The boundaries of that habitat and the characteristics that make it attractive to juveniles remain to be defined. Some basic attributes, such as depth, temperature, substrate, and the general nature of bottom relief, are relatively easy to measure and describe for large areas. Characterization of the habitats used by juvenile lutjanids will improve the ability to assess and manage productive substrate. Ichthyoplankton sampling has yielded relatively few specimens of larval lutjanids (Collins et al. 1980; Leis 1987), and the value of that approach for assessing adult stocks seems limited. A focused program of sampling and monitoring the juvenile population and estimating the available habitat suitable for them may provide more effective indicators of potential recruitment and indicate the prospects for future adult stocks.

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